

Breeding of the Starling (*Sturnus vulgaris*)

Johnny Karlsson

Fine



Department of Animal Ecology
University of Lund, Sweden

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Så oförmodadt detta arbete kommer i dagsljuset; få ofullständigt kommer det ock ur författarens hand. Om Läsaren behagar antaga det senare såsom en följd af det förra; få torde någon grund dertill kunna finnas af bifogade Herrar Kolleganterns åstundan, att få det snart tryckt, och min egen, att icke sent vara Dem nyttig.

Carl P. Ohrling. 1805.

Dissertation
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ABSTRACT

Colonially and solitarily breeding Starlings (*Sturnus vulgaris*) were studied during 1972-1982 in South Sweden.

Pairs fed mealworms during 30 days prior to laying started laying 5 days earlier and laid 4 % heavier eggs than control pairs, but clutch size, nestling weights, and number of fledglings did not differ from those of unfed pairs.

Breeding was highly synchronized; 95 % of all pairs started laying within 7 days (mean). On average, clutch size decreased by 0.35 eggs/day (mean), resulting in a highly synchronized nest-leaving; this phenomenon was termed hypersynchronization and is thought to be an adaptation for reducing predation and nest parasitism. Due to a lack of nest-sites, Starlings often tried to reproduce by laying in the nests of other Starlings. Mostly they removed an egg from the parasitized clutch. The rate of parasitism was 5 % in colonial and 30 % in solitary pairs (means).

Egg weights did not correlate with date of laying or ambient temperature, showed a tendency to decrease with increasing clutch size, and showed a consistent decreasing trend with laying order within the clutch.

Unlike that in some other hole-nesting passerines, the clutch size of the Starling did not vary with the bottom area of the nest cavity.



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☆ Written together with Hans Källander



Förord och Tack

Förord är de ord som kommer före.

Det är allt.

Tack ska vi ha!
Alla! / *Alm*

I alla fall:

Astrid Ulfstrand (konst, figurer m.m.), Staffan Ulfstrand (handledning, initialt), Nils Christian Stenseth (handledning, flyktigt), Per Brinck (handledning, finalt), Ulla Holmberg (litteralt), Hans Källander (altruism), Gunilla Lindquist (utskrift, påfösning) och Ylva Zachrison (utskrift).

Breeding of the Starling (*Sturnus vulgaris*) - summary

Various aspects of the breeding biology of the Starling were studied during 1972-1982 in Skåne, South Sweden. Data were collected from pairs breeding in nestboxes. A colony was established by putting up 45 nestboxes at a farm, while solitarily breeding pairs were distributed among 30 nestboxes in about 40 ha of semi-open grassland. Another set of nestboxes was used for some experiments relating to intraspecific nest parasitism.

The results are presented in the five papers, whose main results and conclusions are summarized here.

Food availability and breeding performance

For about 30 days prior to the start of egg-laying, fifteen pairs of Starlings were offered mealworms in a cup attached to the nestbox. The birds received enough food to cover their daily energy demands. Their breeding performance was compared to that of birds in a nearby control colony.

The fed birds reacted by: (1.) Staying at the nestboxes during most of the time. Non-fed birds are forced to leave the nest-site for most of the day to find areas rich in food. (2.) They started laying eggs five days earlier than unfed pairs. (3.) Fed birds laid significantly heavier (4 %) eggs than unfed birds. (4.) There were no significant differences between fed and unfed pairs with regard to clutch size, nestling weight, or number of fledglings.

Synchronisation of egg-laying

The timing of breeding was highly synchronized both in colonial and solitary pairs. On average, 95 % of all breeding pairs commenced laying within 7 days. During the synchronized period, clutch size decreases extremely rapidly (with 0.35 eggs per day), resulting in an even more synchronized onset of incubation, and, at the end, nest-leaving by the young. This latter way of concentrating the breeding activities into a short period I call hypersynchronization. The adaptive value of synchronizing breeding is thought to be a way of reducing predation risks, particularly after nest-leaving, and of avoiding being parasitized by other Starlings during the laying period.

Intraspecific nest parasitism

Starling eggs are often found on the ground, mostly in the vicinity of Starling nests. Most of these eggs have been thrown out by parasitic Starlings; when laying their own egg in the nest, parasitic Starlings mostly carry away one of the host's eggs. It is shown that intraspecific parasitism is a common breeding strategy in the Starling: pairs nesting colonially suffered a 5 % parasitism (mean for five years) vs. about 30 % for pairs breeding solitarily. Experiments indicate that the parasitic behaviour is an alternative strategy that pairs use when they fail to find a nest-site of their own.

Egg weight variation

Egg weights were studied from several aspects. There was no correlation between egg weight and date of laying, or between egg weight and ambient temperature. There was a tendency towards decreasing egg weight with increasing clutch size, and a consistent trend of decreasing egg weight with laying order within the clutch.

No area-effect on the clutch size

In some passerines there is a positive correlation between clutch size and bottom area of the nest cavity (nestbox). This relationship is not present in the Starling; and it has repeatedly been shown that the Starling is a determinant layer.



Laying date and breeding performance in the Starling, *Sturnus vulgaris*: effects of supplemental food

Inverkan av utfodring på häckningsförloppet hos staren

One can distinguish two main hypothesis concerning the timing of the breeding season in temperate nidicolous birds: (i) the female starts laying eggs in response to some external cue(s) in such a way that the time the young demand most food coincides with the period of highest food abundance (Lack 1954), and (ii) laying starts as soon as the female can accumulate enough energy and nutrient stores for forming eggs (Perrins 1970). A third hypothesis, 'the food stability hypothesis' (Bryant 1975), can be viewed as a variation of Lack's original hypothesis. It states that the female defers laying until the risk of encountering poor feeding conditions during incubation is minimal. It thus differs from Lack's hypothesis only in the critical period to which laying is adjusted being that of incubation, not the nestling period. In both these hypotheses laying is thought to be adaptively timed to external conditions that occur later. In Perrins' 'food limitation hypothesis', however, it is assumed that early breeding is advantageous, i.e. favoured by natural selection, but prevented by the limited food available to the female. It was based on the observations that young Great Tits *Parus major* and Manx Shearwaters *Puffinus puffinus* from early broods survived better than those from late broods (Perrins 1965, 1966).

One prediction from the food limitation hypothesis is that experimental provision of adequate food should result in an earlier start of laying. This prediction has been supported in a number of studies on different species of birds: Carrion Crow *Corvus corone* (Yom-Tov 1974), Great Tit (Källander 1974), Willow Tit *Parus montanus* and Crested Tit *P. cristatus* (von Brömssen & Jansson 1980), Song Sparrow *Melospiza melodia* (Smith et al. 1980), Herring Gull *Larus argentatus* (Spaans in Drent & Daan 1980), Magpie *Pica pica* (Högstedt 1981), Sparrowhawk *Accipiter nisus* (Newton & Marquiss 1981), Kestrel *Falco tinnunculus* (Dijkstra et al. 1982), and Red-winged Blackbird *Agelaius phoeniceus* (Ewald & Rohwer 1982).

In this paper we present results of a food provisioning experiment involving Starlings *Sturnus vulgaris*, carried out in Skåne, South Sweden, in spring 1982.

The Starling is one of the earliest migrants to return to South Sweden in spring, arriving in late February or early March. More or less immediately on arrival, prospective nest-holes are visited and defended against other Starlings. Yet laying does not start until the last days of April or, usually, the first week of May (median date in 7 years varied between 29 April and 7 May; part 3, this thesis). Is this delay caused by an energy shortage of the laying female or is the species' breeding season adjusted, through some external cue, so as to coincide with peak food abundance for the nestlings (or fledglings)?

STUDY AREA AND METHODS

The study was carried out on the Revinge military training area about 20 km east of Lund. The c. 40 km² large area is predominantly grazed, permanent grassland. Starlings are very common, nesting both in colonies and solitarily, on buildings, in tree holes, and in nest-boxes. For this study, two colonies of birds nesting in boxes were used; one (the experimental, called V. Tvet below) was established in 1981 when 16 boxes were erected in a small, open birch grove. The number of boxes was reduced to 15 in 1982, all of them occupied by Starlings. The control colony (Sjötorp) has been monitored since 1973 and comprised 44 boxes with 39 breeding pairs in 1982, the boxes being situated both on the walls of a disused building and in the surrounding trees. Boxes of the same type and dimensions were used in both areas which are 8 km apart.

The Starlings at V. Tvet were fed mealworms (*Tenebrio larvae*) in plastic cups 10 cm wide and 4 cm deep attached to the side of each nest-box. Starting on 2 April, every evening after the Starlings had gone to roost, each container was supplied with about 50 g of mealworms. This ration was increased to about 60 g from 6 April, to 70 g from 9 April, and to about 100 g from 12 April. Provisioning continued until 30 April inclusive when all but two females had started laying.

The Starlings immediately took the mealworms, so that, except after the first day, all cups were empty. Day-time checks showed that all mealworms had been taken already before 11 a.m. Several bird species may eat mealworms, but in our experiment few other

species competed with the Starlings for them. A few mealworms were taken by Great Tits and Chaffinches *Fringilla coelebs*; the main competitors were a pair of Jackdaws *Corvus monedula* that nested close to some of the Starlings. The Jackdaws concentrated their efforts to a few containers closest to their nest and were never observed remaining for long anyway. Although we cannot estimate the impact of these Jackdaws, it can be safely concluded that most of the 3600 g of mealworms that were supplied during the experiment was used by the Starlings.

On the basis of several studies of the daily energy expenditure (DEE), Walsberg (1980) calculated the formula: $DEE \text{ (Kcal/day)} = 11.87 + W^{0.608}$ (W = weight in g).

The mean weight of the Starlings in our study was approximately 82 g, resulting in a DEE of 41.2 Kcal. The energy content of the mealworms used was 4898 cal/g dry weight (37 % of their fresh weight). With a digestive efficiency of 74 % (Taitt 1973) the daily intake requirements correspond to 55.7 Kcal, or 30.7 g mealworms (fresh weight). In feeding trials with mealworms, Taitt (1973) got DEE values of 43.2 and 36.6 Kcal for males (75 g) and females (73 g), respectively. This is close to our value of 41.2 Kcal (for birds with a weight of 82 g) given by the Walsberg equation.

The nest-boxes were checked regularly, and after laying had started the eggs were weighed every or every second day. Nestlings were weighed when 13 days old. The length of the nestling period was not checked in order not to cause premature leaving, but observations from a distance showed that the nestlings at V. Tvet had fledged after the normal time of c. 20 days (during the last days before fledging the entrance hole is more or less permanently occupied by one of the young).

RESULTS

With the benefit of additional food, Starlings were more attendant at their nests, advanced laying, and produced heavier eggs.

Attendance pattern

On each of frequent controls at the experimental colony, Starlings were present at the boxes. This is a remarkable change in behaviour, since, during the pre-laying period Starlings at Revinge are normally not present at the nest for most of the day. Thus,

at three boxes kept under continuous observation in April 1981, the Starlings were away for 73 %, made visits longer than 10 mins during 12 %, and made visits shorter than 10 mins during 15 % of the day-light hours; in the afternoon, the boxes were not visited at all for periods of 4 to 8 hours.

Start of laying

Additional food advanced laying by 5 days (Fig. 1; Mann Whitney U-test, $U = 526.5$, $z = 4.768$, $p < 0.001$). In 1981, when no food was provided, the median date was the same in both colonies (7 May). A comparison of fledging dates in other parts of the Revinge area also supports the conclusion that the extra food we provided advanced laying. Observations, although not carried out systematically, showed that no other Starlings in the area fledged as early as those at V. Tvet. Some variation between nests was observed, but most young fledged at about the same dates as the Sjötorp birds. This was true also of the young in two nests on a building close to the experimental colony.

Our results thus differ from those of Westwood & Dobson (1981) who found that captive Starlings in a late spring delayed laying exactly to the same extent as did free-living birds despite having access to a more than adequate food supply.

Clutch size

Mean clutch size was 5.60 eggs at V. Tvet (S.D. 0.74, $n = 15$) against 5.30 (S.D. 0.81, $n = 37$) at Sjötorp; the difference is not statistically significant (t-test, $p = 0.217$). The larger mean clutch size at V. Tvet is less than that expected from a regression of clutch size on laying date (the slope usually being in the order of 0.35 eggs day⁻¹; part 3, this thesis).

Egg weights

Unfortunately eggs could not be weighed every day so eggs laid on two successive days sometimes had to be weighed on the same occasion. When such weighings included the first (or the last) egg in a clutch, the mean weight of the two eggs weighed together was used in the analysis; this procedure had no influence on the comparisons made here.

The mean weight of the first eggs differed significantly between the colonies as did that of the last eggs and of all eggs

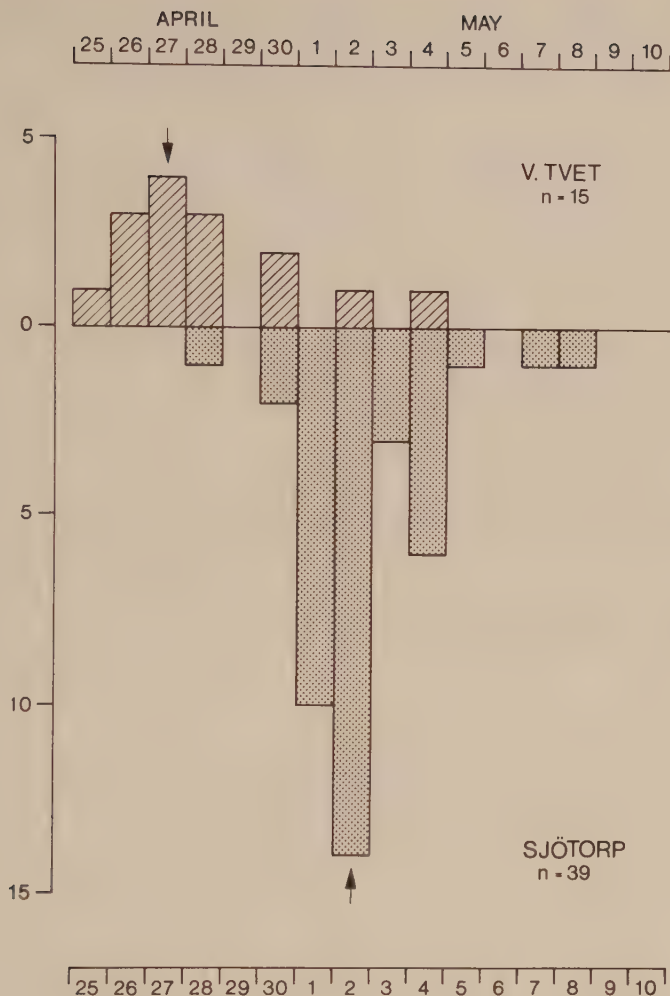


Fig. 1. Laying date of birds provided extra food (V. Tvet) compared with (unfed) controls (Sjötorp). Arrows indicate median date for the first egg in the clutches. The difference, five days, is significant at the 0.001 level (Mann Whitney U-test).

Häckningsstart hos starar som utfodrats med mjölmaskar (V. Tvet) jämfört med kontrollfåglar som inte fått någon extra föda (Sjötorp). De utfodrade fåglarna påbörjade häckningen fem dagar (medianvärden) tidigare än de ofodrade fåglarna. Skillnaden är statistiskt signifikant.

Tab. 1. Egg weights (g) at V. Tvet (experimental) and Sjötorp (control) in 1982. Differences tested with Student's t-test.
Äggvikter (g) vid V. Tvet (experimentgrupp) och Sjötorp (kontrollgrupp) häckningssäsongen 1982. Skillnader prövade med t-test.

	V. Tvet			Sjötorp			Difference	
	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	n	<i>Skillnad</i>	p
First eggs <i>Första äggen</i>	7.57	0.61	15	7.12	0.61	38	0.45	0.020
Last eggs <i>Sista äggen</i>	7.24	0.52	15	6.90	0.50	34	0.35	0.038
All eggs <i>Alla äggen</i>	7.38	0.54	79	6.97	0.54	198	0.41	0.0002

combined (excluding known parasitic eggs), see Tab. 1. Egg weights at both localities decreased by 0.033 g for each day later that the egg was laid, but the decrease was not statistically significant. Even taking this decrease and the difference in laying dates into account, eggs were more than 4 % heavier at V. Tvet than at Sjötorp.

Nestling weights

Nestlings were weighed when 13 days old. The mean weight of 61 young at V. Tvet was identical to that of 104 young at Sjötorp, 73.07 g (S.D. 6.31 and 6.07, respectively).

Mean nestling weight decreased with increasing brood size (V. Tvet: $y = 82.12 - 1.91 x$, $r_{12} = 0.566$, $p < 0.05$; Sjötorp: $y = 75.52 - 0.52 x$, $r_{21} = 0.08$, N.S.), but increased with advancing date (V. Tvet: $y = 70.34 + 0.85 x$, $r_{12} = 0.439$, N.S.; Sjötorp: $y = 57.69 + 2.92 x$, $r_{21} = 0.753$, $p < 0.001$). This trend, i.e. heavier nestlings later in the season, was also noted in 1981 when 69 broods at Sjötorp and surrounding areas were weighed ($y = 69.85 + 0.95 x$, $r_{67} = 0.296$, $p < 0.02$). These positive correlations remain also after the effect of a seasonally decreasing brood size has been removed in a partial correlation.

Fledging success

One of the 15 nests at V. Tvet and 2 of the 39 at Sjötorp failed to produce fledged young. The mean number of fledglings was 4.07 (S.D. 1.71) at V. Tvet and 4.21 (S.D. 1.53) at Sjötorp, while a

mean of 4.36 and 4.43 young fledged from broods that produced at least one fledging young. Neither difference is statistically significant.

DISCUSSION

In this, as in most other provisioning experiments, the predicted advancement of laying was achieved. The question is whether this result should be accepted as evidence in support of the food limitation hypothesis. Critical to this hypothesis is that early laying enhances fitness. This could be brought about by a better survival of young from early clutches (Perrins 1965, 1966, Daan & Dijkstra 1982). This advantage of early laying could, however, not be substantiated for Great Tits (Noordwijk et al. 1981, Källander 1983). In most years, broods from the middle of the frequency distribution of laying dates produced proportionally more recruits to next year's breeding population than did earlier or later broods. Also Parsons (1976), in the Herring Gull, found that young from the middle of the breeding period survived best, and he concluded that, although Herring Gulls would probably be able to lay earlier than they do, there is selection against early breeding.

Perrins (1970) also drew attention to the interesting (and critical) question whether the earliest breeders would increase their fitness even more if they were able to lay earlier still (they should in case earlier breeding resulted in a better synchronisation between critical periods with regard to food demands and food availability). Theoretically at least, the advancement of laying achieved in food provisioning experiments should produce data to answer this question. Unfortunately, the survival to independence of young of experimental and control pairs has not been reported in any of the studies published so far (but cf. Källander 1983, and above). This is true also for the present study, where survival was followed only to fledging. There was, however, no difference in the mean production of fledglings between experimental and control pairs. Differences in nestling weights could be indicative of different survival probabilities after nest leaving (cf. Lack 1948 for the Starling). As noted above, nestling weights on their 13th day were identical in the two colonies. The weight of young of the same age tended to increase with the progress of the season, this increase being statistically significant at Sjötorp in 1981 and 1982. This suggests

that food availability was improving, but, of course, says nothing about the situation later encountered by the fledglings and, therefore, about the optimal timing of breeding.

In summary, the food limitation hypothesis rests on the assumption that an earlier start of egg laying results in increased fitness; for this, however, there is little support in passerines and even data to the contrary.

If we do not accept the food limitation hypothesis, what alternatives could explain the advancement of laying resulting from experimental food supplementation? If birds time their egg laying in such a way that maximum food demands that occur later are to coincide with peak food abundance (Lack 1954), they clearly need some sort of cue that correlates reasonably well with future food availability. The influence of a number of possible, often interdependent, factors has been analysed (day length, Gwinner 1975, temperature, Kluijver 1952, bud bursting, van Balen 1973, Slagsvold 1976; seasonal rains, Immelmann 1971). Jones & Ward (1976), however, studying Red-billed Quelea *Quelea quelea* in two African regions, argued that no external timers or cues were necessary to initiate breeding; laying should start when sufficient protein had been stored. If this mechanism is to work, however, the attainment of sufficient reserves for laying must correlate with favourable conditions for the later raising of the brood, otherwise the young might starve.

A modified version of this idea was presented by Fogden & Fogden (1979), who found a close correlation between the protein level in the flight muscle and the start of egg laying in the Grey-backed Camaroptera *Camaroptera brevicaudata* and reported similar results in other species. They concluded that the protein level at which breeding was initiated had been determined by natural selection so that its attainment predicted suitable future conditions for egg laying and rearing young. Alternatively they suggested the reserve might provide protein for the clutch of eggs. In the first case, a certain threshold value for the protein stores is viewed as a proximate cue on which the birds base their decision to start laying. In the second case, which is identical with that of Jones & Ward (1976), this threshold level may or may not be attained at the most appropriate time. When delayed beyond the optimal point for raising young, the situation is the same as the one Perrins (1970) envisaged in his food limitation hypothesis.

Unfortunately, it does not necessarily follow from the correlation between protein levels in flight muscle and laying dates that the birds are actually using these levels as a proximate cue for when to start breeding; it could be that they start laying down reserves in response to some other cue such as green vegetation. Then, even if laying was triggered at a particular reserve level, the actual timing would be dependent, at least partly, on that other cue. (A reverse example was given by Fogden & Fogden (1979). Reed Warblers *Acrocephalus scirpaceus* in peak protein condition were sometimes forced to delay laying until the new reed that provided nest sites had developed.)

The moderate response to experimental food provisioning (by 2-8 d in tits *Parus* spp. (Källander 1974, von Brömssen & Jansson 1980), the Carrion Crow (Yom-Tov 1974), and the Magpie (Högestedt 1980), led Högestedt (1981) to conclude that some factor other than food determines the onset of laying, and he also presented a graphical model to illustrate the situation. If it is true that some factor other than food, or several factors in combination, is responsible for the initiation of breeding, the attainment of a specific energy or protein level may nevertheless be necessary before laying could start. On this hypothesis, the time taken to reach that level would be dependent on prevailing feeding conditions, i.e. the slope of the curve describing the increments in resource stores would vary. The advancement of laying achieved in food provisioning experiments would thus be explained by the faster attainment of the threshold level by experimental compared to control birds. The slightly earlier breeding observed in warm (Dhondt & Eyckerman 1979) or well insulated (O'Connor 1979) nest-boxes fits the same explanation: although reacting to the same external cues, birds in warm and cool boxes reach necessary resource levels at different times. Also differences between town and countryside (Perrins 1965) could be explained in the same way, but here phenological events also differ. The hypothesis would, of course, also account for differences in territory quality and for differences between individuals. Thus, Högestedt (1974) found a negative correlation between lumbricid biomass and the time Lapwings *Vanellus vanellus* spent on the territory before laying eggs. Individuals who acquire food more efficiently would breed earlier than less efficient ones. In several species, older birds start laying earlier than younger birds (review in Klomp 1970); sometimes this may reflect differences in habitat quality but

this does not affect the argument. It may be significant that food provisioning influenced the start of laying of 1 yr old Great Tits and Song Sparrows more than that of older birds (Källander 1974, Smith et al. 1980). It has been repeatedly observed that birds start breeding earlier in early compared to late springs. This may seem trivial, but at least in the Great Tit (Perrins 1965, van Balen 1973) there is a negative correlation between the warmth sum and the mean laying date (warmth sum is the summed daily temperatures over some specified period prior to laying). This is consistent with the energy/protein threshold level hypothesis, because, even though various phenological events are earlier in milder springs, at least two factors influence the rate of energy acquisition negatively. First, days are shorter and, perhaps more important, nights are longer. Second, as demonstrated by Perrins (1973, Fig. 2), caterpillars grow more slowly when they hatch early; this would lead to a slower increase in available biomass in mild (early) springs.

In summary then, a number of observations indicate that food (energy or protein) influences laying dates. However, they form an insufficient basis for rejecting the original food limitation hypothesis of Perrins (1970). One observation that could do so would be if birds 'lured' to breed earlier could be shown to have lower success than birds in the natural situation; such data remain lacking. The limited advancement of laying following food supplementation provides some support for the idea that, in some species, some other factor (or factors) plays a role in initiating breeding and that the attainment of a particular nutrient reserve level is responsible for the finer tuning of egg laying.

It should, however, be pointed out that the role of food in controlling the onset of breeding was dismissed by van Balen (1973) on the grounds that Great Tits started laying at about the same date in broad-leaved as in coniferous forest despite large differences in food levels. Food availability in the prelaying period has not been measured, however, and differences may be smaller than assumed. Another testable hypothesis is that courtship feeding is more intense in the latter habitat. Thus, ad hoc hypotheses can relatively easily be invented to explain the similar laying dates in the two habitats, but as long as they remain untested, van Balen's (1973) point is challenging.

Not all feeding experiments have yielded the moderate response indicated above. In three studies, the advancement of laying was

more dramatic: about 25 d in the Song Sparrow (Smith et al. 1980), between 12 and 26 d in the Red-winged Blackbird (Ewald & Rohwer 1982), and at least 23 d in the Kestrel (Dijkstra et al. 1982). These results suggest that true differences may exist between species with regard to the factors controlling the timing of their breeding, those responding more strongly to food supplementation possibly being more directly governed by food availability. It is tempting to think that species that base their reproduction on food sources of an unpredictable durability (e.g., those dependent on small rodents whose populations may crash at any time) should react opportunistically and start laying as soon as food conditions permit. This explanation, however, seems to fit neither the Song Sparrow nor the Red-winged Blackbird.

Clutch size

We found no effect of food supplementation on clutch size in the Starlings. This is in agreement with the results for seven out of those eight passerine species so far given extra food prior to laying. Only in the Magpie was a significantly larger mean clutch size reported in one of two years (Högstedt 1981). This apparent absence of effects on the number of eggs laid may indicate that, at least in some passerines, clutch size is not directly related to the feeding conditions at the time of laying, possibly because they poorly predict future food levels. This, of course, would especially apply if the laying female took different kinds of food from that fed to the young. In these species, clutch size is probably genetically adjusted to conditions prevailing in the habitat at the time young are in the nest or to some other later period (although it may be modified in response to e.g., density, as found for the Great Tit (Kluijver 1951, Perrins 1965, and others). The existence of different mechanisms in different passerine species is indicated by the work of Jones & Ward (1976) on *Quelea* and by Fogden & Fogden (1979) on *Camaroptera brevicaudata* and on *Acrocephalus scirpaceus*; in the former species clutch size seems to be determined by female intake rate, in the latter two this does not seem to be the case.

In contrast, in the two non-passerines studied, the situation was different. Sparrowhawks in a poor habitat that were given additional food even produced larger clutches than (unfed) Sparrowhawks in a rich habitat (Newton & Marquiss 1981). Kestrels also laid larger clutches after food supplementation but of a

size expected from the advanced laying date and the seasonal trend in clutch size (Dijkstra et al. 1982). Positive correlations between clutch size and food abundance have also been reported in a number of other raptors (see Klomp 1970, Newton 1979). In the Kestrel, Daan & Dijkstra (1982) worked out an elegant model for the relationship between food, time of laying, and clutch size. The model depends on there existing a positive correlation between female reserve acquisition rate (which is largely dependent on male courtship feeding performance) and capacity later to raise the brood; such a relationship was found (Daan et al. in press).

Egg weight

Eggs in the experimental colony were 4-5 % heavier than eggs in the control (Tab. 1), no doubt an effect of the additional food that experimental birds received. In the other studies, only Högestedt (1980) presented data on egg weight; experimentally fed Magpies laid eggs 6-9 % heavier than did control birds. Further, although more indirect, evidence that feeding conditions affect egg weights exists in the form of laying gaps (zero weights) in adverse weather (Winkel 1970), and correlations between egg weight and ambient temperature (Jones 1973, Ekman et al. in prep.). A positive correlation between egg weight and lumbricid biomass was found in the Fieldfare *Turdus pilaris* (Otto 1976).

Jones (1973) and Howe (1976) expressed similar views as to the relationship between the resources available to the female and the size (weight) of her eggs. When enough food is present she lays, but when less is available than necessary for forming an egg of a certain minimum size (probably determined by the survival chances of the young it contains) she refrains from laying. When more resources are available than necessary to attain this size, at least part of them are channelled into the egg as extra nutrients; positive correlations between egg weight and subsequent growth and survival of the young have been established in several species (Shifferli 1973, Parsons 1970, 1975, Howe 1976, O'Connor 1979, Lundberg & Väisänen 1979, Ankney 1980). The increased egg weight resulting from feeding experiments agrees with this explanation, but, although most plausible, the existence of a minimum egg size remains to be demonstrated; this could be done if egg size distributions were truncated on the lower side.

The contribution to the forming egg from daily food intake and from internal stores may vary between species (Fogden & Fogden 1979). One prediction that can be made is that laying gaps due to temporary feeding difficulties (adverse weather) should not usually occur in species depending on internal stores; in these species, such difficulties should result in a reduced clutch size (see Jones & Ward 1976).

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SAMMANFATTNING

Tillgången på mat påverkar fåglarnas äggläggning. Det är t.ex. viktigt att det finns gott om mat för boungarna, för de utflugna ungarna som börjar bli självständiga, för de ruggande föräldrarna eller för honan som skall producera äggen. Det är många, kanske varandra delvis motverkande faktorer som påverkar resultatet. I denna uppsats redovisas försök med att tillföra extra mat under ca en månad före äggläggningen, för att se hur näringstillgången under den tiden kan påverka äggläggningens början osv. Vid 15 holkar serverades mellan 50 och 100 gram mjölmaskar i skålar som fästes på holkarna. Stararna åt villigt av födan. För att täcka dagsbehovet av energi behövde en stare ca 31 g mjölmaskar. De matade stararna reagerade genom att: (1.) Börja häcka 5 dagar tidigare än övriga starar. (2.) Medelkullstorleken påverkades inte signifikant (5,60 för utfodrade, 5,30 för övriga). (3.) Lägga ca 6% tyngre ägg. (4.) Vikten på ungarna och antalet utflugna ungar påverkades inte. (4.) Ingen signifikant påverkan på ungar-nas vikt eller antalet utflugna ungar.



Synchronisation of breeding in the Starling, *Sturnus vulgaris*

Synkronisering av häckningen hos staren

"It is one of the major facts of natural history that most living organisms reproduce at some particular season of the year. The time at which the young are produced usually coincides with the season of abundant food supply for either the parents, the offspring, or both." This citation from the classical book "Bird flocks and the breeding cycle" by Fraser Darling, may well serve as a starting point to this chapter on the synchronisation of breeding in the Starling.

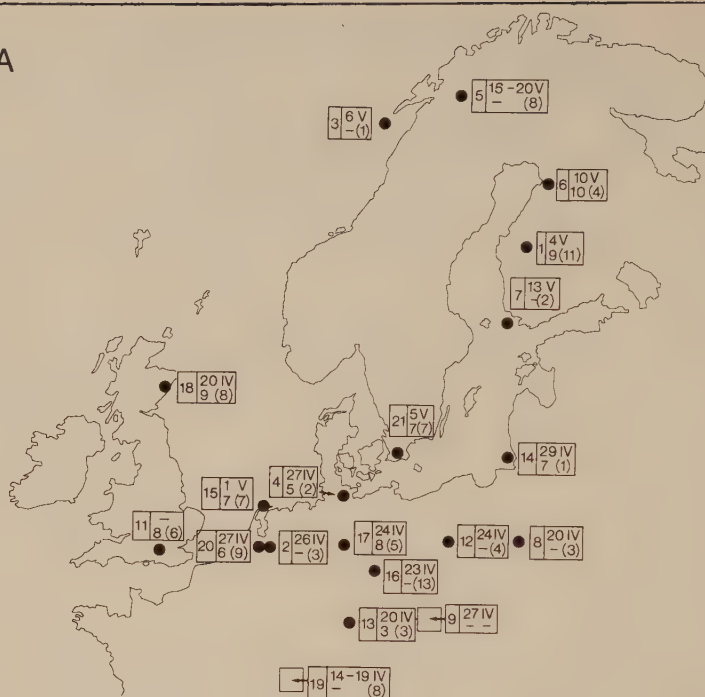
The term synchronisation is used to describe the phenomenon that practically all pairs within a population, or within an area, breed almost simultaneously. For the Starling, this means, as will be shown below, that almost all birds within an area start laying eggs within about a week.

After an introductory paragraph, in which I present data on breeding synchronisation of the Starling in Europe, the results of my own studies are analysed. In that part of the paper, I introduce the term 'hyper-synchronisation' for the fact that, during the already highly synchronised laying period, the Starlings attain an even more pronounced synchronisation of the nestling period and of fledging date by each female laying progressively fewer eggs for each day later that her clutch is initiated.

INTRODUCTION

Within the European distribution range of the Starling, which extends from the Pyrenees (43° N) to North Cape (71° N), there is about a score of studies that can be used to analyse the degree of synchronisation of laying, clutch size, and the frequency of second clutches (see legend to Fig. 1 for references). Most of these studies emphasize the remarkable degree of synchronisation of laying. I define the synchronised laying period as the period within which clutches are started with, at most, one day's gap

A



B



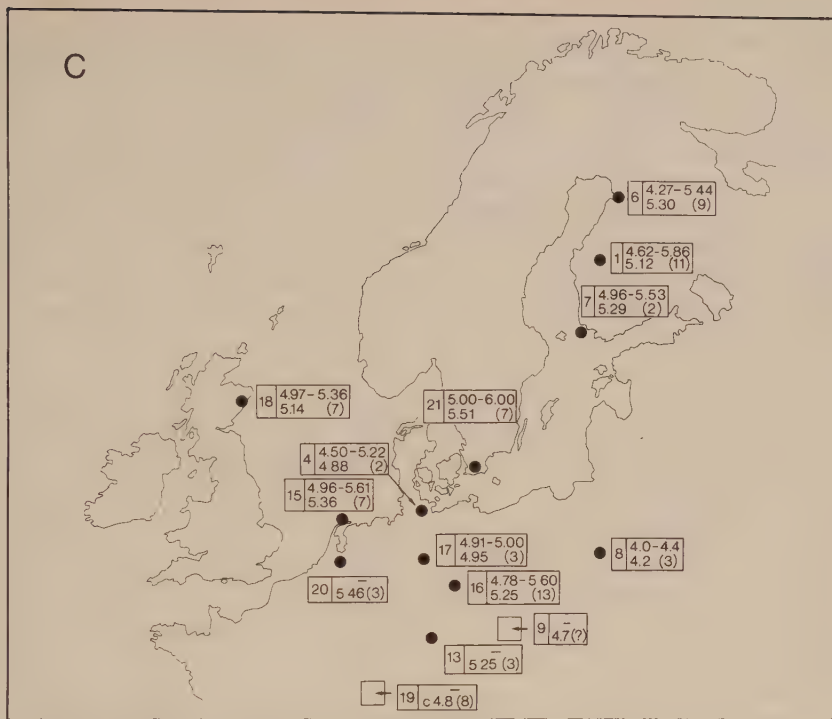


Fig. 1. Summary of some parameters of the breeding of the Starling in Europe. The maps are based on data from the papers listed below. Black dots indicate study sites. In two cases, data refer to entire countries as indicated by open squares; this applies to Switzerland (ref. No. 19) and Czechoslovakia (refs No. 9 and 10). In each rectangle, the number to the far left corresponds to the number in the reference list.

1A. Synchronization and time-table for the onset of egg-laying. The top row in each rectangle gives the median date of the synchronized period, while the bottom row give the mean duration of the synchronized period (in days) together with the number of study years (in brackets). Missing information indicated with a dash. (IV = April, V = May.) The synchronized period of laying is defined as the period within which there is at most one day without any new clutch being commenced.

1B. Proportion (%) of true second clutches (in some studies hard to evaluate!). When available, information about range of variation is given in brackets. + indicate that second clutches occur, but proportion unknown.

ctd

1C. Mean clutch size (bottom row) together with yearly variation (min- and max-values recorded in each study; top row). Number of years in brackets.

References: 1. Korpimäki 1978, 2. Westerterp 1973, 3. Wagner 1958, 4. Haarhus 1968, 5. Andersson & Müller 1978, 6. Ojanen et al. 1979, 7. Tenovuo & Lemmetyinen 1970, 8. Luniak 1977, 9. Pikula & Folk 1970, 10. Havlin & Folk 1961, 11. Feare & Burham 1978, 12. Bogucki 1972, 13. Wallraff 1953, 14. Schüz 1943, 15. Tinbergen 1981, 16. Schneider 1972, 17. Berndt 1939, 18. Dunnet 1955 and Anderson 1961, 19. Schifferli 1957, 20. Kluijver 1933, 1935, 21. own data.

På kartorna redovisas uppgifter om starens häckningsbiologi i Europa, som den speglas i de undersökningar som redovisas i referenslistan ovan. Numret till vänster i datarutorna hänvisar till nummer i referenslistan.

1A. Övre uppgiften i datarutan anger medianvärdet för äggläggningens början och i den undre raden anges medelvärde för längden (dagar) på den synkrona äggläggningen. Inom parentes anges antalet studieår.

1B. Förekomsten (%) av andrakullar. Ett + innebär att andra-kullar förekommer men frekvensen är okänd.

1C. Medelvärde för kullstorlek (undre värdet) och max/minvärde under studieperioden. Antalet studieår inom parentes.

between them. With my definition, the total period during which clutches were initiated, varied from 3 to 10 days, with a mean of 7 days (Fig. 1A). This degree of synchronisation of first clutches occurs in all the investigated populations, even in those where the total breeding period includes the rearing of a second brood (Fig. 1B); apparently, in Europe at least the length of the synchronised period does not vary between areas.

The frequency of second clutches shows a strong correlation with the time at which first clutches are started (Fig. 2, based on data from Aberdeen and Leipzig, respectively; Dunnet 1955, Anderson 1961, Schneider 1972). A good illustration was also provided by a study on the island of Schiermonnikoog (Tinbergen 1981). In eight years, second broods occurred only in one year (1977), when the median laying date for the first clutches, 26

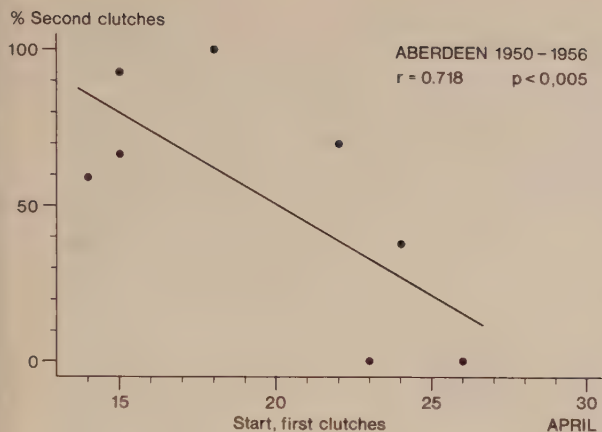
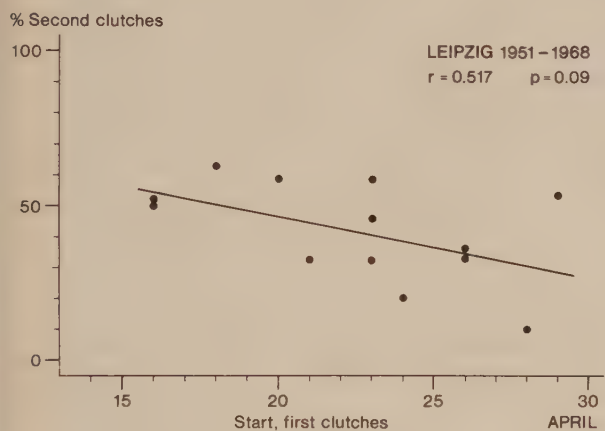


Fig. 2. Frequency of second clutches in relation to median date for the first clutches laid within the synchronized period. Data for Aberdeen from Dunnet (1955) and Anderson (1961), and for Leipzig from Schneider (1972).



Frekvensen andrakullar i förhållande till median-datum för förstakullarna under den synkroniserade perioden. Uppgifter från Aberdeen har hämtats ur Dunnet (1955) och Anderson (1961) och för Leipzig ur Schneider (1972).

April, was five days earlier than the median date for all the years, and c. 70 % of the pairs laid a second clutch.

One can divide Europe into three zones with regard to the frequency of second clutches; their approximate limits are indicated in Fig. 1B. On the European mainland, except for the northernmost part, at least a proportion of the Starlings lay a second clutch. In a transition zone, which includes the northern parts of West Germany, the Netherlands, and parts of the United Kingdom, second clutches are laid only in the early, or earliest years. North of this transition zone, there are, according to studies from Schleswig-Holstein, Sweden and Finland, with one notable exception, no second clutches at all. On the Lofoten

Fig. 3. Map showing the study area, the military training field Revingehed. A colony of Starlings was established in 1972 at an abandoned farm (marked with a rectangle) immediately to the west of Lake Krankesjön. It contained 30 nestboxes during the first two years (1972-73); another 15 boxes were added in 1975. The bottom figure gives details about the location of each nestbox (arrows). Eighteen of the boxes were put up on the buildings, and the rest in the tall trees surrounding the farm. The top figure is a detail of the area to north of the lake, and shows the location of the 30 solitary nestboxes put up in 1975.

Karta över undersökningsområdet, beläget på det militära övningsfältet Revingehed. En koloni med starar skapades 1972 genom att 30 holkar sattes upp vid en övergiven gård (markerad med en fyrkant omedelbart väster om sjön). Nedtill på kartan visas en förstoring över koloniområdet och holkarnas placering (pilarna). Arton holkar sitter på byggnader, resten i de höga träd som omger gården. Det inramade området norr om sjön visar placeringen av solitärholkarna (markerade med nummer på förstoringen av området överst i figuren).

islands (alt. in the coastal areas of the extreme north-west of Norway), however, the Starlings are non-migratory and also show a high frequency of second clutches (Wagner 1958, P. Lundberg pers. comm.).

Fig. 1C gives data on the regional variation of clutch size of the Starling in Central and North Europe. The smallest clutches are found in the central parts of the Continent (Switzerland and Czechoslovakia) and the largest clutches in the Netherlands, southern Sweden, and Finland. There is no consistent trend in clutch size, neither with latitude nor with longitude (see e.g., discussions in Lack 1947, Cody 1971, and Slagsvold 1975). The mean size of first clutches in the three zones, distinguished above on the basis of their different proportions of second clutches, was 5.22 for the northern zone (with no second clutches), 5.15 for the transition zone, and 4.94 (zone with second clutches), but the considerable variation and the overlap in clutch size between study sites in different zones make discussions of regional trends speculative and conclusions uncertain.

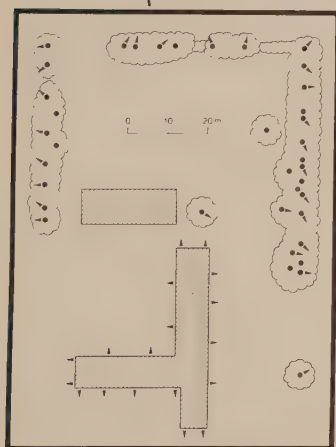
-  Coniferous wood
-  Deciduous wood
-  Wet meadow on peat soil
-  Ungrazed meadow on mineral soil
-  Open field on mineral soil
-  Open marsh
-  Pond
-  Village

1 km

0 500 m

Lake
Kranke-
sjön

Lake
Krankesjön



STUDY AREA AND METHODS

The study was carried out on the Revinge military training area about 20 km east of Lund, South Sweden (approx. $55^{\circ} 43' N$, $13^{\circ} 30' E$). The area consists of permanently grazed grassland interrupted by small woods and tree plantations. An eutrophic lake, Krankesjön, is situated in the middle of the area. See Fig. 3 for details about the area and the location of the nestboxes used in this study.

In 1972 a colony of Starlings was established at an abandoned farm, Sjötorp. In this and the following year, the colony held 30 nestboxes, but from 1974 it was enlarged to 45. In 1975 another 30 nestboxes were put up along the northern side of the lake (see Fig. 3) with inter-individual distances long enough to prevent their occupants from seeing or hearing each other. In the following account these nestboxes are called solitary in contrast to the ones at the colony.

The nestboxes were made of wood with an inner bottom area of 12 x 12 cm. The depth from the centre of the entrance hole (50 mm in diameter) was 31 cm. The boxes were put up at a height of 4 m. They were inspected at least daily during the egg laying and hatching periods.

In the years 1974 to 1977, the nestboxes in the colony were used for experiments as follows: during all four years 15 boxes were "shrunked" to a bottom area of 10 x 12 cm, 15 were of the normal size and 15 (the new boxes put up in 1974) measured 15 x 15 cm. These manipulations were made in order to investigate if the area-effect on clutch size (Karlsson & Nilsson 1977) is present also in the Starling (results presented in Part 6, this thesis); as no difference in clutch size was found between nestboxes of different size, the data are used also in this analysis of synchronisation. In 1976 I made an egg-removal experiment in the colony in an attempt to prolong the laying period of the earliest breeders. The second and third eggs were thus removed from the 20 earliest clutches. The Starlings did not react to these losses during laying. I therefore include the data here. The clutch size used is the number of eggs actually laid in each nestbox.

In known cases, parasitic eggs are not included in the clutch sizes used in the calculations.

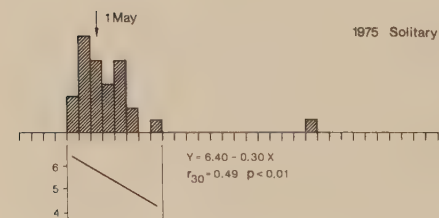
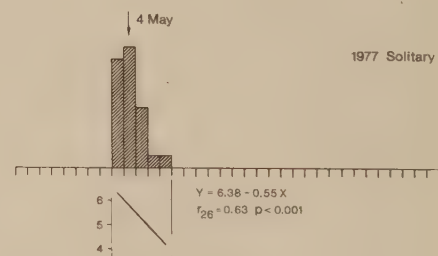
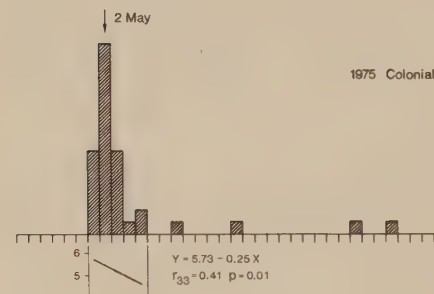
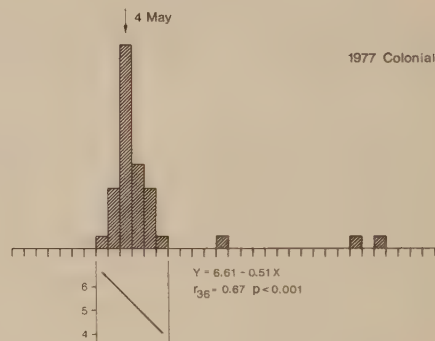
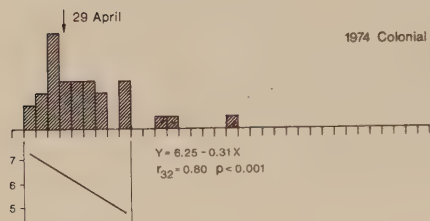
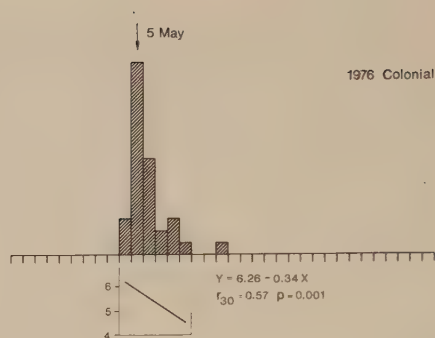
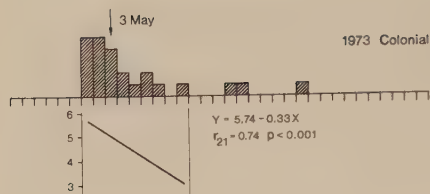
RESULTS

The highly synchronized breeding pattern in the Starling, described in the introduction to this paper, holds true also for the Starlings I studied. The dates of laying and the length of the synchronized period in each of the years 1973-1981 are shown in Fig. 4. In the colonial pairs the synchronized period varied from 5 to 10 days and in the solitary pairs from 5 to 9 days. Its mean length over all the years was c. 7 days, a value close to those recorded in other studies in Europe (see Fig. 1A). The median date of the synchronized period varied from 29 April (in 1974) to 7 May (1981). Data about the synchronization are summarized in Table 1. The reasons for the differences between years in the timing of laying will not be considered in this paper (but see the discussion in Part 2 of this thesis).

Table 1. Data about the synchronization of the breeding of colonial and solitary Starlings at Revinge. n = number of clutches commenced within the synchronized period. k = number of clutches started outside the synchronized period. b = decrease in clutch size per day during the synchronized period (slope of the regression line for clutch size on laying date).

Uppgifter om synkroniseringen hos koloni- och solitärhäckande starrar i studieområdet på Revingefältet. n = antalet påbörjade kullar inom den synkrona perioden. k = antalet kullar utanför den synkrona perioden. b = kullstorlekens minskning per dag (lutningen för regressionen mellan kullstorlek och häckningsstart inom den synkrona perioden).

Year	Colonial pairs					Solitary pairs				
	n	k	Synchron. period			n	k	Synchron. period		
			Date	Days	b			Date	Days	b
1973	21	3	1-9 May	9	0.33	-	-	-	-	-
1974	32	3	26 Apr-4 May	10	0.31	-	-	-	-	-
1975	35	4	1-5 May	5	0.30	30	1	29 Apr-6 May	8	0.25
1976	30	1	4-9 May	6	0.34	-	-	-	-	-
1977	38	3	2-7 May	6	0.51	25	0	3-7 May	5	0.55
1980	35	4	1-6 May	6	0.28	26	0	30 Apr-6 May	7	0.24
1981	41	1	6-10 May	5	0.39	30	0	4-12 May	9	0.33



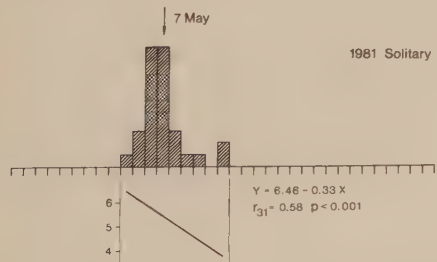
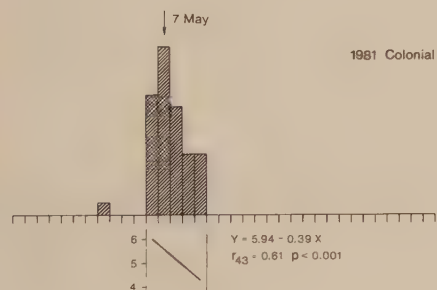
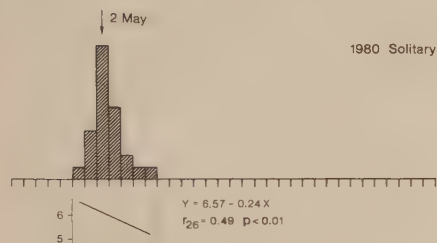
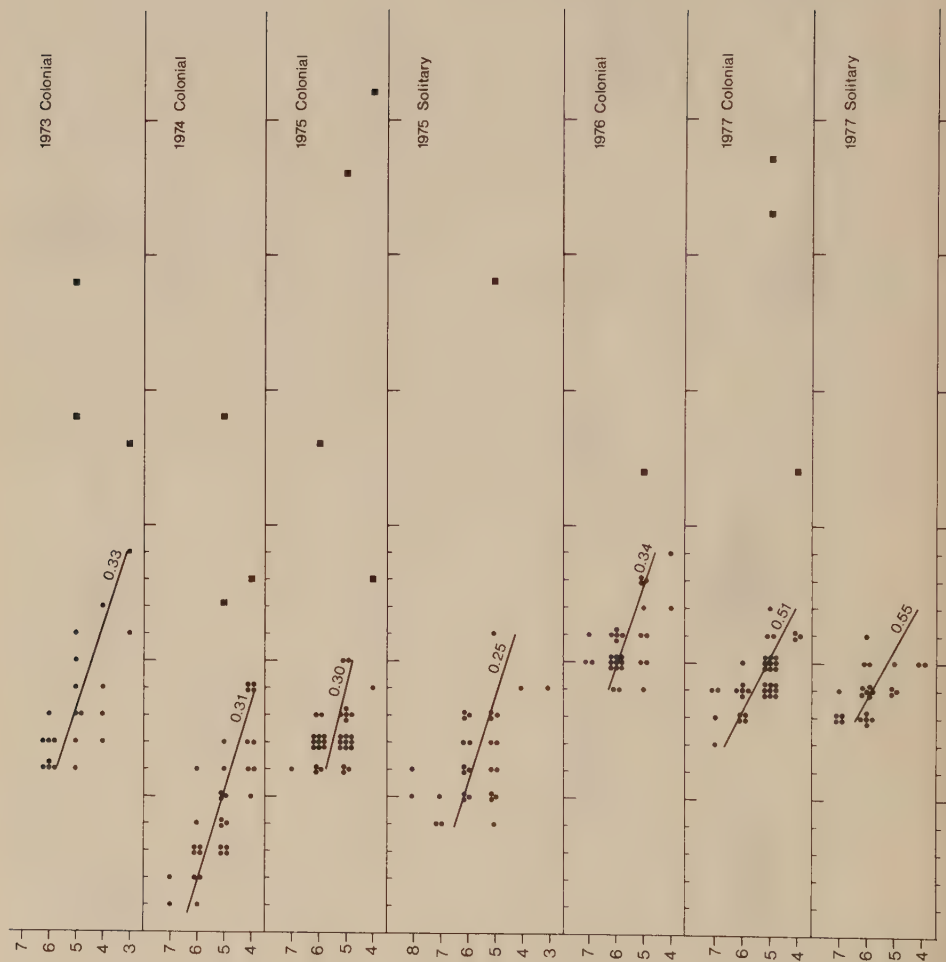


Fig. 4. Synchronization of the breeding in colonial and solitary Starlings at Revinge. The synchronized period of laying is defined as the period within which there is a maximum of one day without any new clutches being commenced as indicated by the diagrams below the abscissa. Median date within the synchronized period is shown with an arrow, and the equation for the regression of clutch size on laying date is given for each year.

Synkronisering av äggläggningen hos kolonilevande och solitärlevande starar. Den synkrona perioden definieras som den period inom vilken det maximalt finns en dag utan någon påbörjad kull. Mediandatum inom den synkrona perioden är markerad med en pil. Ekvationerna för regressionslinjerna har första läggningsdagen som noll. Se också figur 5, där regressionerna presenteras utförligare.



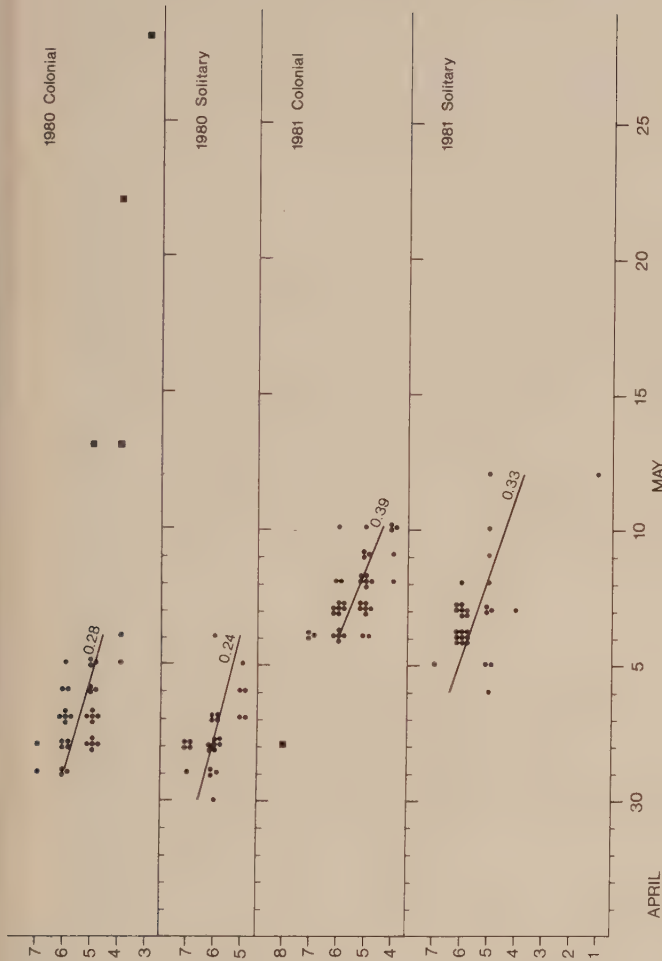


Fig. 5. The relationship between clutch size and onset of laying in each year for colonial and solitary Starlings at Revinge. The slope of the linear regression is indicated on each line. The equations, r - and p -values are given in Fig. 4. Squares show clutches started outside the synchronized period. They are not included in the regression analysis.

Samband mellan kullstorlek och start för äggläggningen. Regressionslinjens lutning anges på linjen för respektive år. Linjernas ekvationer, korrelationskoefficienter (r) och sannolikhetsvärden (p) finns i Fig. 4. Kullar som påbörjades utanför den synkrona perioden är markerade med kvadrater. De senare kullarna är ej inkluderade i regressionsanalyserna.

Table 3. Proportion of nestboxes occupied during the entire study at Revinge, 1973-1981. The colonial nestboxes were studied in 7, and the solitary nestboxes in 4 seasons. The colony held 45 nestboxes (30 in 1973) and the series of solitary boxes 30 in all years. *Beläggningen i holkarna under åren 1973-1981. Koloniholkarna kontrollerades under 7 och de solitära holkarna under 4 säsonger. Kolonin omfattade 45 holkar (dock endast 30 år 1973) och den solitära holkserien 30.*

	Nestboxes available Total for all years (7)	Occupied by syn- chronized broods	Nestboxes still available*	Broods outside synchr. period
Colonial	298	232 (78 %)	66	19 (29 %)
Solitary	115	111 (97 %)	4	1 (25 %)

* Most occupied by unmated birds.

All linear regression of clutch size on laying date reveals a steep decrease. The regression equation for each year is given in Fig. 4, and the slopes of the regression lines are also indicated in Fig. 5. The decrease is significant at the 1 % level in all cases. Clutch size and date of laying for all the clutches are given in Fig.

Close to 100 % of all nestboxes were occupied, but the frequency of clutches laid was considerably lower (Tab. 3).

DISCUSSION

Group stimulation as a factor influencing breeding events in birds has for long been named the "Fraser Darling Effect" after F.F. Darling, who in his book from 1938 on the function of bird flocks, made explicit suggestions about the ecological significance of flocking in birds. He proposed that the synchronous breeding in colonial birds, in some way(s) is stimulated by interactions between the birds. He also suggested, that the intensity of group stimulation should increase with increasing colony size. Thus, the degree of synchrony would be more pronounced the larger the colony ("social stimulation may be density-related").

Darling, and most later students of the topic, concentrated on colony breeders such as gulls and auks; evidence in favour of the "Fraser Darling Effect" in these species has gradually accumulated. It has repeatedly been shown that: (a) many seabirds and other colonial species are more synchronized within a colony than

between colonies; (b) a colony can be divided in sub-colonies that are synchronized in relation to each other; (c) pairs living in a colony start egg-laying earlier; (d) pairs living in the middle of the colony produce more offspring compared to more peripheral pairs; (e) pairs "working" in the middle of the synchronized period do better than other pairs; (f) different types of behaviour (wing-flagging, courtship, calls etc may stimulate other individuals to perform the same behaviours. Effects of group stimulation have also been shown experimentally, e.g. in the Ring Dove (*Streptopelia risoria*; Lott et al. 1967). Immelman (1971) gave a concentrated review of group stimulation as did Ashmole (1963), Crook (1964), Patterson (1965), Southern (1974), and Ravelling (1978).

Yom-Tov (1975) argued that some of the positive effects of synchronized breeding that have been identified in colonial species are likely to be beneficial also to territorial birds. In a study of the Carrion Crow in Scotland, he showed that synchronization (and production of young) increased with increasing density of nests. Yom-Tov meant that the crucial factor in the case of the Carrion Crow was intraspecific predation on eggs and young. Other similar factors that may lead to synchronized breeding in territorial species are, e.g. intraspecific nest parasitism (ducks) and nest destruction (the Rook).

Synchrony in the Starling

Regardless of how we define "synchronous breeding", it is obvious that the Starling is a species where breeding is highly synchronized. This has been shown of colonially breeding Starlings in Europe. Apparently synchronized breeding is also a normal phenomenon in the introduced, and nowadays wide-spread Starling in North America (Kessel 1957). My own data from Revinge (Figs 4 and 5) also show a high degree of synchronization; in all, only 19 clutches (7.6 %) out of 251 laid in the colony were started outside the synchronized period. These "late" clutches were always started in nestboxes which had been occupied during the synchronized period, apparently by males failing to attract a mate until late in the season. It is well known from other studies in Europe that there is a surplus of males. The females are more interesting, however. Do they represent birds that breed in their first year, or are they birds that have been parasitizing others during the

synchronized period and move in to lay and incubate for themselves later?

Hypersynchronization

The extremely rapid decrease in clutch size during the synchronized period is far beyond what is considered a "normal" decrease in clutch size with the progression of the season (which is in the order of 0.05 egg/day, sometimes 0.10; see examples given in Tab. 2). Second clutches of Great Tits in South Sweden provide an extreme example, explained as an effect of rapidly diminishing food levels (Källander 1983).

My opinion is, that the rapid decrease in clutch size with season observed in the Starling, is an adaption aiming at concentrating the fledging period even further. The only Starling data available for comparison are those of Ojanen et al. (1979) and Korpimäki (1978) from Finland, but these authors calculated the decrease over too long periods. However, Ojanen et al. (1979) made calculations separately for first clutches (nearly three weeks time) and found a relatively strong decrease of 0.11 eggs/day as compared with 0.04 for the whole season. Their data indicate that the situation in Finland may be similar to that at Revinge, with a rapid decrease in clutch size during the "synchronized" period (lasting for 10 days in the study of Ojanen et al.; see Fig. 1A).

Experiments to induce the Starlings to alter their clutch size have always failed, which provides good evidence for the Starling being a deterministic layer. I experienced this myself when I tried to prolong the laying period of the earliest birds by removing the second and third eggs in each clutch. The idea behind this experiment was that the late birds were somehow influenced by the earliest birds to cease laying approximately at the same time as the earliest birds. Then, if it were possible to prolong the laying period of the earliest birds by one or two days, the late birds should also continue laying for another day or two. As said earlier, the experiment failed, since the birds losing eggs did not react, but apparently laid clutches of normal size.

There seems to be two ways in which the birds could attain the observed hypersynchronization. One is that late layers resorb eggs and lay smaller clutches. The other is that birds that lay small clutches delay the onset of laying.

Tab. 2. Some species of birds lay progressively smaller clutches as the season proceeds, while clutch size in other species may increase, be constant or show some other pattern; see Klomp (1970) for a review. This table gives some examples of the magnitude of the decrease in clutch size with time for some well-studied species, to be compared with the data on the Starling presented in this paper. b = slope of linear regression line; eggs d^{-1} .
Kullistorleken avtar med häckningstidens framskridande hos en del fåglar, medan den hos andra ökar, är konstant eller visar något annat mönster (se Klomp 1970 för en översikt). I tabellen nedan ges några exempel på kullistorlekens variation med tiden hos några välstuderade arter, att jämföras med motsvarande uppgifter för staren som presenteras i denna uppsats. b = lutningen på regressionslinjen (antal ägg per dag).

Starling	$b = 0.06$	Pooled data for 12 years, all clutches	Finland	Korpimäki 1978
<i>Sturnus vulgaris</i>				
-"	0.11	First clutches (3-22 May), nine years combined	Finland	Ojanen et al. 1979
-"	0.04	All clutches, incl. those laid after 22 May		-"
-"	0.35	Mean for the synchronized period, all years combined	Sweden	This study
Maggie	0.02	Pooled data for several years, all clutches	Sweden	Högstedt (pers.comm.)
<i>Pica pica</i>				
Fieldfare	0.02	Whole country, nestrecord cards	Finland	von Haartman 1967
<i>Turdus pilaris</i>				
Pied Flycatcher	0.07	Mean value for 25 years	Finland	-"
<i>Ficedula hypoleuca</i>				
Great Tit	0.11	Mean value	Great Britain	Perrins 1979
<i>Parus major</i>	± 0	Mean value, first clutches	Sweden	Källander 1983
Blue Tit	0.40	Mean value, second clutches		
Blue Tit	0.05	Mean value	Sweden	Perrins 1979
<i>Parus caeruleus</i>				

Why synchronization?

When discussing the capacity of birds to do the same things at the same time, it is worth pointing out the often remarkable synchronization of migratory activities (as emphasized by Wynne-Edwards 1962). This is worth bearing in mind when discussing breeding activities, since the factors influencing migratory readiness and the cues the birds use may resemble those involved in breeding, e.g. nutritional state, day length, temperature, weather conditions, and the social influence from other birds present.

The following explanations of synchronous breeding have been put forward (several of them more or less interrelated):

1. To permit the immediate formation of flocks after fledging (Dunnet 1955).
2. To reduce the risk of predation on eggs or nestlings (Darling 1938), and on the fledglings.
3. To reduce the risk for intraspecific interference, e.g. predation or parasitism.
4. To permit a more efficient exploitation of food (Dunnet 1955).
5. Synchronous breeding is simply an effect of the limited time available for breeding, a situation well-known from arctic habitats, which may, however, also apply to tropical areas with seasonal rains. Example of extreme synchronization is found in arctic geese (Hohn 1957, Lemieux 1959, Ryder 1967, Ravelling 1978).

Most of the above examples of benefits connected with synchronized breeding have been advocated for the Starling. The presumed positive effects of flock living are the reduced risk of predation and an enhanced rate of food intake. Support is available for both arguments. In an aviary experiment Powell (1974) showed that Starlings in a flock of ten spent only 12 % of their feeding time in surveillance compared to 47 % when feeding alone. A positive correlation between rate of food finding and flock size (at least up to a certain flock size) has been shown for several bird species (Krebs 1974, Krebs & Barnard 1980).

The risks for predation on eggs or nestlings (point 2 above) is not very likely to apply in the case of the Starling, because, as a hole-nester, its nest is relatively predator safe.

The frequent intraspecific nest parasitism (see part 4, this thesis) may also influence the degree of synchronization in the Starling (point 3 above). Synchronous laying by all pairs in a population reduces a parasitic individual's chances of placing her eggs in other birds' nests compared to a situation where the egg-laying period is more extended.

How is synchronization achieved?

The question of how the Starlings synchronize breeding has already been touched upon in the discussion of hypersynchronization above. As shown in part 3 in this thesis, Starlings breeding solitarily are synchronized to the same degree as those living in colonies. Thus, there is no reason to believe that, as is the normal for colonial birds, that they are synchronized through activities within the colony.

Starlings are highly sociable, during most of the year roosting and feeding together, often in huge concentrations. In my study area, large numbers of Starlings fly to the nearby lake for the night. Up to the beginning of egg-laying, they also feed together in flocks, the solitary breeders taking part in these social events to the same degree as the colonial birds. Thus, all the Starlings breeding within a large area may be considered as belonging to a super-colony due to their "colonial" habits during the night and most of the day.

Further, it may well be, that the pre-roost aerial displays may serve to synchronize activities. Perhaps these displays are modified in some way prior to the beginning of egg-laying. It is at least easy to imagine how the rapidly decreasing number of participants in the roosting flocks may act as reliable indication that egg-laying has started.

One can conclude by saying that factors such as day-length and temperature act as hour-hand, yearly variations in weather and food as minute-hand, and social behaviour as second-hand in the synchronization of breeding in the Starling.

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SAMMANFATTNING

Staren har en starkt synkroniserad häckning. Inom ett område börjar nästan alla paren att lägga ägg inom loppet av några dagar. Detta mönster finns i hela Europa (se Fig. 1). I undersökningsområdet på Revingefältet i Skåne varade den synkrona starten av häckningen i medeltal 7 dagar (se Tab. 1). Se också Fig. 1, där synkroniseringen presenteras grafiskt.

Under den synkrona perioden minskar kullstorleken mycket hastigt med tiden, i genomsnitt med 0,35 ägg per dag (se Fig. 2.) Denna hastiga minskning leder till att kläckning och utflygning blir än mera synkrona än äggläggningens start.

Synkroniseringen är sannolikt ett sätt att motverka predation efter det att ungarna har lämnat boet, eller ett sätt att minska riskerna att bli parasiterad av andra starar. Båda faktorerna kan naturligtvis spela in.

Stararnas sociala samvaro, t ex vid övernattningsplatserna förmodas spela en viktig roll som synkroniserande faktor.



Intraspecific nest parasitism in the Starling, *Sturnus vulgaris*

Staren som boparasit på stare

There are many peculiarities in the breeding system of the Starling. Some have for long been misinterpreted, others, fortunately enough, remain to be revealed. In this chapter I will present data on intraspecific nest parasitism, but I find it appropriate to begin with a short review of what is known about the parasitic behaviour and some related aspects of the breeding biology of the Starling.

INTRODUCTORY NOTES

Intraspecific nest parasitism

For a long time, instances of intraspecific nest parasitism seems to have been considered as mistakes ('freak eggs', 'egg dumping'). In a review of brood parasitism in birds, Payne (1977) says that "about 1% of all bird species are brood parasites" (on other species), while "intraspecific parasitism is uncommon in birds". This statement is surprising, since it has long been well-known that e.g. several species of Anseriformes lay eggs in the nests of other individuals of their own species. No less than 32 species of Anseriformes (i.e. 21% of all species in that order) were thus listed by Yom-Tov (1980) in a review of intraspecific nest parasitism in birds. In all, he mentions intraspecific nest parasitism in 53 species of birds (i.e. in about 0.6% of the existing species). Yom-Tov comments this list by saying that many more species are suspected of intraspecific nest parasitism on the basis of records of extraordinarily large clutches, but were omitted because the evidence was considered to weak. It thus seems that there are at least as many intraspecific as interspecific nest parasites in birds.

In his review, Yom-Tov argues that the parasitic females may be of three kinds: (1.) Unmated, mostly young females, who copulate with mated males; (2.) Females who have lost their nests; (3.) Mated females who occasionally lay in the nests of other females. A fourth alternative, however, seems most reasonable, namely true parasitic pairs, where also the male shares the parasitic habit.

Evidence for intraspecific nest parasitism

Starlings lay one egg per day. Thus, when two or more new eggs appear in a nest on the same day, it is a good evidence for more than one female being involved in the laying.

The occurrence of extra eggs was mentioned by Kluijver (1933, 1935), but considered to be mistakes. Kluijver also noted that eggs sometimes disappeared from the nestboxes, often lying on the ground beneath. He explained such irregularities as a result of interference from unmated males present at nearby nestboxes.

Good indirect evidence for a rather high rate of nest parasitism is found in the often-cited paper by Lack (1948) on "Natural selection and family size in the Starling". The high number of large clutches and broods in his data is obviously a result of parasitism.

Further evidence for nest parasitism in the Starling, although either not discussed, or misinterpreted, by the authors, is found e.g. in the papers of Dunnett (1955), Kessel (1957), Anderson (1961), Royall (1966) and Bogucki (1972). The data in Dunnett (1955) and Anderson (1961) were later re-evaluated by Yom-Tov et al. (1974), and they reported that no less than about 40% of the nests seemed to have been parasitized. Later studies in Great Britain by Evans (1980,ms) and C.J. Feare (unpublished) have confirmed that intraspecific nest parasitism is a widespread phenomenon in Starlings in Great Britain.

Polygami and three birds at the same nest

Normally Starlings are monogamous, but there are many reports of exceptions from this rule. Thus reports of males having two females simultaneously in different nestboxes are frequent (Freitag 1936, 1937, 1939, Schüz 1943, Wallraff 1953, Kessel 1957, Schifferli 1957). Kessel (1950) gives an extreme example from the United States, where a male had five different females in the course of the breeding season, three of them simultaneously and in different breeding stages.

The occurrence of bigyny in the Starling, and even polygyny, is somewhat surprising, since an excess of males has been reported in all breeding populations studied (10 to 40 % more males than females). (In some papers, a mate shift between successive clutches in the same season has erroneously been regarded as poly-

gamy.) Feare & Burham (1978) report, that mate shifts are common, as are changes of nesting site, between first and second clutches. Therefore one cannot assume that one has to do with true second breedings in all cases where a new clutch appear in a nestbox soon after the fledging of the first brood.

A special polygamous constellation is when three birds are present at the same nest. This has been reported several times in the Starling (Grabham 1895, Newstead 1908, Kluijver 1935, Anderson 1961). Groups of three birds are a rather common sight in South Sweden, especially during the pre-laying period, but unfortunately I lack quantitative data on this phenomenon. Anderson (1961) reported that one trio consisted of two females and one male. (During the time when young are in the nest, foreign Starlings rather often visit nests, and sometimes even enter them (see Kessel 1957).)

The presence of three individuals at a nest, who take part in the rearing of the young, may be a form of bigamy, but if so, one might ask, if the third bird is a female, where she has laid her eggs. One explanation could be, that she has parasitized other pairs, but this seems unlikely. I find it more probable that the third bird is present as a helper at the nest. The presumed helpers may be related to the pair which they help (e.g. non-breeding offspring from the previous year) or their aid is an investment that increases their chances to take over a suitable nestplace, either later in the same season or in future seasons. The benefit to the host of accepting a helper could be that it allows rapid remating in case one of the birds in the pair (of the right sex!) dies, the aid in guarding the nest against intruders (for example parasitic Starlings) that the helper provides, or the food it collects for the nestlings.

The Starling as an interspecific nest parasite

It has often been stated, that interspecific nest parasitism has evolved via intraspecific parasitism (Payne 1977). It is therefore interesting to look at cases of Starlings laying in the nests of other species: (a.) a pair of Bluebirds (*Sialia sialis*) reared two Starling chicks together with four own young (Musselman 1942); (b.) one Starling egg was found in a clutch of four in a nest of the Pileated Woodpecker (*Dryocopus pileatus*; Hoyt 1938); (c.) one Starling egg was likewise found in a clutch of seven in a Magpie (*Pica pica*) nest (Andrews 1915); (d.) a Starling and a Stock Dove

(*Columba oenas*) laid in the same nest (Hewett 1881); (e.) a common Mynah (*Acridotheres tristis*) raised a young Starling (Wilson 1979); (f.) finally an observation from my own study area may be mentioned: a Starling tried to enter the nest of a Great Spotted Woodpecker (*Dendrocopos major*). The owner was at home and the intruder was repulsed, and just in the moment of take off, "laid" an egg, that fell to the ground (I.Rudebeck, pers.comm.).

STUDY AREA AND METHODS

The study was carried out in the Revinge area (see Part 3 for a more detailed presentation).

Data on the frequency of the nest parasitism were obtained in the colony at Sjötorp and in the solitary nestboxes to the north of Lake Krankesjön (see Fig.3 in Part 3). The nestboxes were checked at least once a day during egg-laying and the ground below the nestboxes was searched for eggs. Some of the solitary nestboxes were also used (in 1982) for an experiment where extra eggs were added to some clutches in order to see if their owners reacted to the presence of strange eggs (simulated parasitism). Normal eggs were added to five, and eggs painted with black spots to seven nestboxes.

In 1981, an experiment was designed in order to see how parasitic Starlings would react if supplied with non-guarded nestboxes in which laying had just commenced. New nestboxes were put up in the wood to the north of the solitary nestboxes (Fig. 3, Part 3) and five boxes were later selected for the experiment. In the evening following the laying of the second egg, each nestbox was moved to a tree at a distance of 10 to 30 m from its original position. One of the eggs was left in the nestbox. A new nestbox with a "handmade" nestcup was placed in the original position, and one of the eggs left in the nest. The events during the next days were carefully recorded.

RESULTS AND DISCUSSION

Frequency of parasitism

Data on the frequency of parasitism at Revinge are presented in Tab. 1 and Fig. 1. Three conclusions can be drawn from the data:

- (1.) A large part of the population is parasitized, and intra-

Tab. 1. Frequency of nest parasitism in colonial and solitary Starlings at Revinge. A clutch is classified as parasitized if one or more eggs has been removed or added, or if eggs have been found beneath the nestbox (the latter eggs may be the host's egg, or the result of an aborted attack from a parasitic bird. "Not occupied" means that no Starlings were present at the nestbox. Nestboxes occupied (mainly by males; details unknown), but clutches not laid, are not included in the table. See also Fig.1 for a graphic presentation.

Frekvens parasitism i koloni- och solitärholkar på Revingefältet. En äggkull betecknas som parasiterad om ett eller flera ägg har tillkommit eller försvunnit, likaså om ägg har hittats under holken. "Not occupied" innebär att inga starar har funnits vid, och försvarat holken. Övriga holkar (ej med i tabellen) har varit upptagna av i huvudsak hannar (detaljer ej kända). Se också Fig. 1 för en grafisk presentation.

	Number of nestboxes	With clutches %	Not occupied %	Clutches parasitized %
<u>Colonial nestboxes</u>				
1972	30	73	0	4.5
1973	30	80	3.3	0
1974	45	78	?	0
1975	45	82	0	8.1
1976	45	76	11.1	0
1977	43	84	9.3	0
1980	45	89	0	7.5
1981	45	98	0	9.1
1982	44	91	0	20.0
<u>Solitary nestboxes</u>				
1975	30	100	0	36.6
1977	28	100	0	7.1
1980	27	96	0	26.9
1981	30	100	0	36.6
1982	27	100	0	44.4

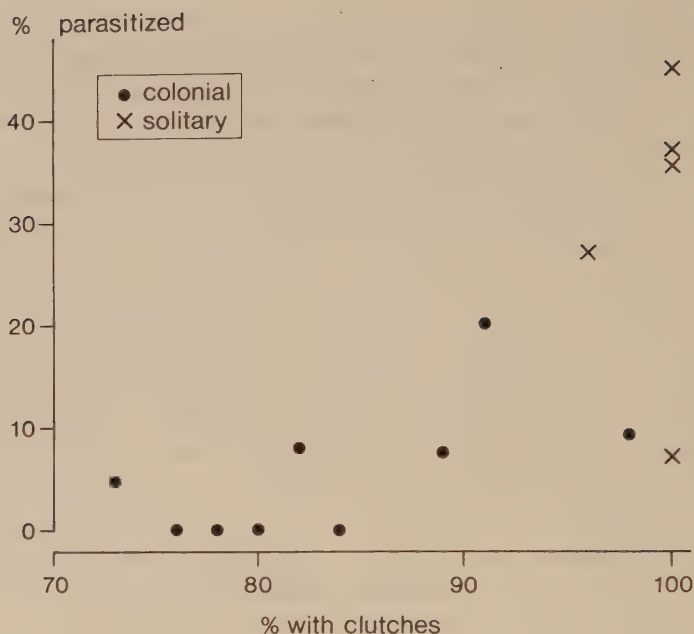


Fig. 1. Frequency (%) of intraspecific nest parasitism in the Starling at Revinge in relation to population density, measured as the % of available nestboxes containing clutches. C.f. Tab. 2.

Frekvens (%) inomartsparasitism hos starrar på Revingefältet i förhållande till populationstäthet (mätt som % av antalet tillgängliga holkar som har kullar).

specific nest parasitism seems to be a regular breeding strategy in the area.

(2.) The frequency of parasitism is much higher in solitary than in colonial nests.

(3.) There is a clear correlation between population density and the rate of parasitism.

The frequency of parasitism varied from 0 to 20 % in the colonial birds, with a mean of c. 5% for the nine years (1972-1982) of study. Corresponding values for the solitary birds (five years: 1975-1982) was 7 to 44 % with a mean of c. 30%. If the comparison between colonial and solitary nests is restricted to years from which data are available from both categories (1975-1982), the percentage of parasitism is 9 versus 30 %. Thus, there was a 3.8 higher risk of being parasitized when breeding alone as compared to breeding colonially.

The only explanation of the different rates of parasitism that I can provide is that pairs breeding in the colony help each other in detecting and chasing parasitic birds that try to enter the colony. If so, one might expect it to be selectively advantageous to obtain a nest site in a colony compared to nesting solitarily. At least if my speculations above about "third birds" acting as helpers (guarding against parasitic birds) are correct, one would predict that solitarily breeding pairs should be more willing to accept helpers compared to colonial birds. But, as a matter of fact, the frequency of third birds may be higher in the colony, which could explain the lower incidence of parasitism there.

Parasitism in relation to population density

Data on the frequency of unoccupied nestboxes are available from 8 years in the colony (Tab. 1). In three of these (1973, 1976, 1977) between 3 and 11% of the nestboxes were unattended (while the other nestboxes were either occupied by a pair or a single bird (male)). In these three years (low population density) no parasitism at all occurred in the colony. Unfortunately, data from the solitary nestboxes are only available for one of these low-density years, but in that year (1977), they experienced the lowest frequency of parasitism recorded in the study (see Tab. 1). Unoccupied nestboxes were never found among the solitary boxes. Fig. 1 gives a graphical presentation of the frequency of parasitism in relation to the number of pairs present.

Who is removing eggs from the nests?

The frequent observations of Starling eggs below, or in the vicinity of nests (and indeed also in places fairly long away from any nests) has often been reported. There are, however, very few observations of how the eggs find their way from the nests to the places where they are found. Berglund (1975) describes how eggs were thrown out, and Evans (ms) observed a Starling leaving a nestbox with an egg in its bill. Thus, there is no longer any doubt that Starlings have the ability to pick up eggs in a nest and carry them away. The remaining uncertainty concerns, whether it is the nest owner (discriminating against foreign eggs) that removes eggs from its own nest, or if it is the parasitic bird that does so. (It is almost exclusively in nests disturbed by parasitic

Tab. 2. Results of experimental parasitism at Revinge in 1982. In 5 of the 27 solitary nestboxes normal eggs (collected in two of the other nestboxes; B below) were added on 5 May. On 6 May eggs painted with black spots were added to 7 nestboxes. In the latter case eggs found outside nestboxes were used. Events in the experimental nestboxes are shown under the heading A below. The laying was followed in the rest of the 27 solitary nestboxes, and irregularities were recorded in 6 (heading C below), while laying was regular in 9 nestboxes. i = number of eggs in the nestbox; o = number of eggs found on the ground outside the nestbox; e = experimental eggs added (+) or taken (-).

Försök med experimentell parasitering i solitärholkar 1982. Normalfärgade ägg placerades i 5 holkar den 5 maj och svartprickiga ägg i 7 holkar den 6 maj. Resultatet framgår av A. i tabellen nedan. Ägg för experimenten hämtades den 5 maj ur två holkar (B. nedan) och i övrigt användes ägg som hittades på marken. Under punkten C. redovisas lägningsstörningar i omanipulerade holkar. i = ägg i holken; o = ägg på marken utanför holken och e = tillagda experimentägg (+) eller borttagna (-).

birds where eggs are removed.) The suspicions, of course, are towards the parasite, since egg removal is a well-known behaviour in some interspecific nest parasites.

In order to solve the question, parasitism was simulated in ten nestboxes in 1982; in some nestboxes I added normal eggs and in some aberrant eggs (spotted black). The results of this experiment are given in Tab. 2. There is no longer reason to get into details in the result (see comments to Tab. 2). The main result was that the (simulated) parasitic eggs were not removed in any of the ten nestboxes. I find this result conclusive enough to claim that it is not the host, but the parasitic bird that removes egg from the nest it parasitize. This is not invariably done, however.

Who is parasitizing? And why?

Are some Starlings parasitic while others are not? Stated otherwise, is there a balanced dimorphism in the reproductive behaviour of the Starling. The results presented above, showing a density dependent frequency of parasitism speaks against the existence of exclusive parasites and in favour of a flexible strategy.

Nestbox no	4 May		5 May			6 May			7 May	
	i	o	i	o	e	i	o	e	i	o

A. Experimental eggs added; normal on 5 May, spotted black on 6 May

61	2	0	2	1	+1	5	0	0	6	0
68	2	0	3	0	+1	5	0	0	6	0
74	1	0	3	0	+1	5	0	0	6	0
60	1	1	2	0	+1	5	0	+1	7	0
71	1	0	2	0	+1	4	0	+1	6	0
49	2	0	3	0	0	4	0	+1	6	0
51	0	0	1	0	0	2	0	+1	4	0
59	0	0	1	0	0	2	0	+1	4	0
62	0	0	1	1	0	1	0	+1	3	0
69	0	0	0	1	0	0	0	+1	0	0

B. Eggs removed on 5 May

63	5	0	5	0	-2	3	0	0	3	0
64	6	0	7	0	-3	4	0	0	5	0

C. Non-manipulated nests with irregularities in laying sequence

48	0	0	1	1	-	0	0	-	0	0
50	3	0	6	0	-	7	0	-	8	0
52	1	0	0	5	-	0	0	-	0	0
53	0	2	0	2	-	1	0	-	2	0
73	3	1	4	0	-	5	1	-	6	0
75	0	1	0	0	-	1	1	-	2	0

Comments to Tab. 2.

61. One egg outside, one missing in the box on 5 May. One parasitic egg on 6 May. 74. One parasitic egg on 5 May. 60. One egg outside on 5 May; One parasitic egg on 6 May. 62. One egg outside on 5 May; One egg missing completely on 6 May. 69. One egg outside, none inside the box on 5 May; The spotted experimental egg missing on 7 May. 48. One egg outside on 5 May and one in the nestbox on 5 May, none left next day. 50. 2 parasitic eggs on 5 May. 52. Extreme case! 5 eggs outside the nestbox on 5 May. At a maximum 2 of these from the nestbox' owner. 53. 2 eggs outside on 4 and 5 May, then normal laying during the two following days. 73. 2 eggs found outside. 75. 1 egg outside on 4 May, no egg at all on 5 May, 1 in the box and 1 outside on 6 May.

Tab. 3. History of events in experimental nestboxes in 1981. In six cases the original nest boxes with their nests were exchanged with new nestboxes containing an artificial nest cup. One of the two eggs in the original nestbox was transferred to the new nestbox which was put up in the original position. The original nestbox was then placed 10-30 m away from its original position, still containing one of the two eggs. The owners of the original nestboxes accepted the shift and continued the breeding activities.

Utvecklingen i experimentholkar 1981. I sex fall omplacerades holkar när två ägg hade lagts och ersattes med nya holkar i vilka en konstgjord balle hade gjorts. Ett av de två äggen placerades i ersättningsholken som sedan sattes upp på den ursprungliga platsen. Originalholkarna sattes upp 10-30 m bort från ursprungspositionen. Ett av äggen fanns kvar i holken. Fåglarna accepterade holkbytet och fortsatte häckningen i de nya holkarna.

Nestbox	Put up at	What happened?
B"	9 May	Nothing. The egg disappeared on 12 May.
E"	8 May	Nothing. Pied Flycatcher started building a nest on 16 May.
F"	9 May	Birds present in the morning of 10 May. Built a new cup covering the egg. First egg on 11 May. Clutch size:3. Young fledged.
G"	9 May	Birds present in the morning of 10 May. New cup built, the egg had disappeared. First new egg laid on 11 May. Clutch size:3. Robbed just prior to hatching.
L"	8 May	Birds present at the nestbox in the morning of 9 May. The original egg was thrown out during the day. A new cup was built within a couple of days, and the first egg was laid on 13 May, and on 14 May the first egg had disappeared. A new clutch was commenced on 15 May. Clutch size:5. Four young fledged.

In order to get information about the behaviour of parasitizing Starlings I made an experiment (1981) in which unguarded nestboxes were offered to the birds. The nestboxes showed all signs of being inhabited by other Starlings. The result is presented in Tab. 3. Of the five nestboxes offered, three were immediately

occupied by what was apparently mated pairs of Starlings, since (in two cases) they were able to lay their first egg in 24 hrs. I find it most probable, that the Starlings that accepted the nest-boxes, which were provided in the middle of the synchronized laying period, were birds that would otherwise have tried to parasitize other Starlings.

Thus, to conclude, my opinion is that the parasitic behaviour found in the Starling is an alternative that can be used when a pair does not succeed in obtaining a nest box in a particular season.

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SAMMANFATTNING

Det är inte ovanligt att man hittar starägg liggande rakt fram på marken. Dessa ägg har tidigare tolkats som nödvärpningar eller av "misstag" utkastade ägg. Under de senaste åren har det emellertid visats, att dessa ägg i stor utsträckning är medvetet bortförda ur holkarna av starar som parasiterar, dvs lägger egna ägg i andras holkar. Under åren 1972-1982 har denna inomartsparasitism studerats på Revingefältet i Skåne. Resultaten kan sammanfattas i följande punkter:

1. Parasitägg förekom ofta i starholkarna. I holkar som satt utspridda (isolerade från varandra) var i genomsnitt 30% parasiterade. Holkar som satt nära varandra och bildade en koloni var parasiterade till ca 5%. Anledningen till skillnaden förmodas vara, att stararna i kolonin försvarar sig gemensamt.

2. År då det fanns holkar lediga (låg populationstäthet) var antalet parasiterade holkar betydligt lägre än år då alla holkar var upptagna. Parasitbeteendet tolkas som en effekt av brist på bohål.

3. Under läggningstiden erbjöds holkar med bobale och ägg i. Holkarna försvarades inte av andra starar. Hälften av holkarna togs omedelbart i besittning av starar, som inom loppet av ett dygn hade byggt ett nytt bo och lagt det första ägget.

4. När ett parasitägg tillkommer i en holk försvinner det ibland ett ägg, så att kullstorleken förblir oförändrad. För att testa om det är holkens ägare eller den parasiterande staren som bär ut ägget, placerades dels normala ägg, dels svartprickiga ägg i 5 resp. 7 holkar. Inga av äggen blev utkastade av holkinnehavarna. Resultatet kan ses som ett gott bevis för att det är de parasiterande stararna som bär ut ägg.



NÄR STARARNA SAMLAS

Den som en oktoberkväll färdas utmed vägen, som följer Våmbsjöns västra strand, skall få se en syn, som han sent skall glömma: hur stararna samlas på kvällen. Redan en timme före solnedgången komma de utmed stranden från trakterna i söder och norr. Det är små flockar om tjugo—trettio, sällan flera, starar men de komma tätt. Mittför den stora ladan mötas de och samla sig till en enda stor flock. Oupphörligt strömma starar till, de komma med en egendomlig flykt, som de endast bruka ha vid färder till och från nattkvarteret. Det visslar i vingarna på dem på ett liknande sätt som hos knipor. En del stryka fram utmed gårdsgården eller vasstopparna och kasta sig plötsligt upp och försvinna i den stora flocken. Andra komma farande högt uppe och slunga sig ned med ett brus, som hörs lång väg. Den väldiga flocken, i vilken ständigt nya uppslukas, håller sig timvis svävande över vassbältet. Än är den klotformig, än långsträckt och spolformig, än drar den ut sig till ett långt slingrande band. Fram och åter svävar den över vassen, tills den vid solnedgången slår ned. Då försvinner den med en gång som på en given signal.

Nu är det, som om det sjöd i en jättekittel. De tusen och åter tusen stararna, talrika såsom vasstråna själva, förena sitt kvitter och sorl till ett mäktigt brusande, som skulle kunna komma en att tro, att allt vatten därinne i vassen råkat i uppror och sjöd.

När mörkret sänker sig över sjön, konturerna börja suddas ut och de sista försenade stararna i brådskanie flykt kommit ilande och försvunnit i den sjudande massan, då blir det tyst, endast vindens rasslande i vassbladen hörs, men i örnen susar det ännu, när man vandrar tillbaka — det är svårt att glömma en sådan kväll, en sådan upplevelse som stararnas flykt vid nattkvarteret.

På våren syns emellertid ingen vass i Våmbsjön. Den, som ej skördats för att användas till rörmattor, skäres ned av isen, när denna bryter upp. Under vårenflyttningen samlas därför alla starflockarna i Krankesjön och vissa är allra mest i Fönesjön. Nu är det heller inte så stora skaror, som när ungfåglarna samlas på hösten, men de måste dock räknas i tusental, och ännu i början av maj, då de skånska stararna börjat sin häckning, övernatta ett par tusen i Fönesjön.

Helt tomt från dem är det aldrig. Vid juni månads början ha t. ex. 700 räknats en morgon. Och efterhand som ungfåglarna komma ut, växa flockarna; redan i juli och sedan ända ut i oktober måste de alltid räknas med femsiffriga tal.

Tar det lång tid för dem att samlas på kvällen, så går uppbrottet på morgonen så mycket snabbare. Ofta lyfter nästan hela skaran på en gång med ett fruktansvärt dån, delar sig och far i långa, glesa band ut över trakten. Men ibland stiger den som ett klot rakt upp ett stycke, hejdar sin stigning, klotet blir ihåligt på mitten och blir till en ring, som växer och fortplantar sig över hela sjön, som ringarna efter en sten, som kastats mot en vattenyta.

Under klar himmel brukar uppbrottet ske just i soluppgången. Jag tillbragte under en vecka i juli 1927 nätterna bredvid lägerelden på stranden. Varje morgon vaknade jag av gryningsljuset en stund före soluppgången, och regelbundet kommo då alltid starflockarna susande förbi utmed stranden en stund senare, just när solskivan stack upp vid horisonten. Senare har jag vid sex olika tillfällen antecknat det klockslag, då huvudflocken har lämnat Kranke- eller Fönesjön, och det visar sig, att fyra av dessa praktiskt taget på m i n u t e n stämma med solens almanacksenliga uppgång, även om den har dolts vid horisonten av moln.

Egg weight variation in the Starling *Sturnus vulgaris*

Variation i äggvikt hos staren

INTRODUCTION

Variations in egg dimensions have for long attracted much interest among oologists, but not until recently has the adaptive significance of this variation been studied (e.g., Parsons 1970, Nisbet 1973, Schifferli 1973, Davis 1975, Howe 1976, 1978, Lundberg & Väisänen 1979, Rydén 1978, O'Connor 1979). In this paper we report on egg weight variation in the Starling (*Sturnus vulgaris*) and discuss the pattern found, especially with regard to egg weight in relation to laying sequence.

STUDY AREA

The study area, Revinge, some 20 km to the east of Lund in southernmost Sweden, consists of permanent natural or seminatural grassland used as a military training area but open to public access. For most of the year large herds of beef cattle graze the major part of the area. Consequently it is an ideal habitat for the Starling which breeds abundantly on buildings, in trees, and in nestboxes. Nearly 100 boxes have been put up for study purposes in various parts of the area. Most of the data presented here come from two colonies: Sjötorp, established in 1972 when 45 boxes were erected, and V. Tvet, established in 1981 (15 boxes). Additional data originate from solitary pairs in boxes scattered with long intervals to the north of Lake Krankesjön in the northern part of the area.

METHODS

In 1981, all eggs of 73 clutches were individually weighed with a spring balance to the nearest 0.1 g on the day after clutch completion. In 1982, the eggs of 15 clutches at V. Tvet and 39 at Sjötorp were weighed during the laying period. Unfortunately the eggs could not be weighed every day, so often two eggs were weighed on the same day. Eggs were dyed with a felt tip-pen enabling eggs already weighed to be distinguished.

At V. Tvet mealworms were provided for about three weeks prior to the start of egg laying. This treatment advanced laying by

about 5 days relative to the Sjötorp colony and resulted in 4-5 % higher egg weights (this thesis, part 2). Provision of mealworms stopped on 1 May; less than 29 % of the eggs were laid after that date.

For the analyses presented below egg weights from 1982 were normalized by using the deviation in weight of each egg in the clutch from the clutch mean. This procedure eliminates the effects of inter-clutch variation and makes the eggs from the two colonies comparable. In cases when two eggs were weighed on the same day the deviation of their mean weight was used; their laying date was considered the mean of the two days on which they were actually laid.

Intraspecific nest parasitism is fairly common in the Starling (Yom-Tov et al. 1974, this thesis, part 4); known parasitic eggs (and parasitised clutches) were excluded in the analysis.

Laying date and clutch size

Median date for the laying of the first egg in the clutch varied between 29 April and 7 May in seven years from which data exist (this thesis, part 1), being latest in 1981. In 1982, it was 2 May at Sjötorp.

At Revinge the clutch normally contains between 3 and 7 eggs, most often 5 or 6. Clutches of 8 or 9 eggs are sometimes found but may be the result of nest parasitism. Parasitism, of course, also occurs in smaller clutches and may go unnoticed even when the eggs are being marked, i.e. if the parasitising female happens to replace the last-laid (unmarked) egg before the daily nest inspection. Variation introduced in this way is likely to be unimportant, however, and could hardly affect the clutch size observed.

In 1981, mean clutch size was 5.42 (S.D. 0.77), excluding two clutches containing 8 and 9 eggs, respectively, and, in 1982, 5.6 at V. Tvet and 5.3 at Sjötorp (this thesis, part 2).

Length of laying period

The start of laying is highly synchronized in the Starling (Kluijver 1933, Dunnet 1955, Korpimäki 1978, Ojanen et al. 1979, Tinbergen 1981, this thesis part 3). Occasionally, however, clutches are laid well outside the normal laying period, e.g., after the desertion of a nest or the death of the hatchlings.

Such clutches, which are rare, were excluded in this study. Of 73 clutches studied in 1981, 77 % were initiated within 3, 85 % within 4, and all within 9 days. In 1982, at Sjötorp 69 % of the 39 clutches were started within 3, 85 within 4, and all within 11 days. At V. Tvet, corresponding figures were 60 % within 3, 87 % within 6, and all within 10 days (15 clutches; see Fig. 1 in part 2, this thesis). Since clutch size in the Starling decreases very strongly with date, e.g., by 0.35 eggs d^{-1} at Revinge in 1981 (this thesis part 3), the total laying period is short. Thus, in 1981, the first egg was laid on 2 May, the last egg of the latest clutch on 15 May ($n = 73$ clutches). The period was similar in 1982: 13 days at Sjötorp and 14 days at V. Tvet. The implication is that effects of laying date on egg weights are likely to be small and difficult to detect.

RESULTS

Egg weight in relation to date of laying

In 1981, the mean weight of the eggs increased by 0.08 g d^{-1} ($n = 72$ clutches; $r = 0.241$, $p < 0.05$). No doubt this was an effect of the strong decrease in clutch size with date combined with a negative relationship between egg weight and clutch size (see below); the correlation disappears in a partial correlation with clutch size kept constant. In 1982, no statistically significant trend was found at neither Sjötorp ($- 0.025 \text{ g d}^{-1}$) nor at V. Tvet ($- 0.004 \text{ g d}^{-1}$). Also a more careful analysis where the deviation of each egg's weight from the clutch mean was related to its date of laying, and where each egg in the laying sequence was treated separately, failed to detect any consistent trend. The slope of the regressions were usually positive, but close to zero.

Egg weight in relation to ambient temperature

Variations in egg weight (deviations from clutch mean) were correlated with daily ambient temperatures (recorded at Malmö airport about 20 km to the south of the study area) on days 1 to 7 before the eggs were laid; this analysis failed to reveal any dependence of egg weight on temperature.

Egg weight in relation to clutch size

A regression of mean egg weight on clutch size showed a statistic-

Tab. 1. Mean egg weights (and S.D.) in g for clutches of different size (1).

Medelvikt (g) hos ägg i kullar av olika storlek.

	Clutch size	$\bar{x}$	S.D.	n
1981:	4	7.02	0.39	7
	5	7.03	0.40	26
	6	6.88	0.55	30
	7	6.87	0.43	4
1982,				
Sjötorp:	3	6.04	-	1
	4	-	-	-
	5	7.00	0.46	19
	6	7.11	0.56	10
	7	6.75	0.25	3
V.Tvet (2):	5	7.55	0.65	5
	6	7.28	0.45	6
	7	6.91	-	1

(1) A calibration of the spring balance showed that the weights given should be reduced by 0.7 g to obtain the true weights.

(2) Egg weights at V. Tvet influenced by feeding experiment (see this thesis, part 2 and text above).

ally significant decrease by 0.124 g egg^{-1} in 1981 ($r_{71} = -0.239$, $p < 0.05$). In 1982, there was a decrease at V. Tvet by 0.296 g egg^{-1} and an increase by 0.087 g egg^{-1} at Sjötorp, but neither correlation was close to statistical significance. The mean egg weight in clutches of different size is given in Tab. 1; none of the differences between means is statistically significant (t-test), but there is some indication that the largest clutches have the lowest mean egg weights.

Egg weight in relation to position in the laying sequence

The deviation in weight of each egg from the clutch mean was plotted for each position in the laying sequence, separately for clutches of 5, 6, and 7 eggs (Fig. 1; values based on means of

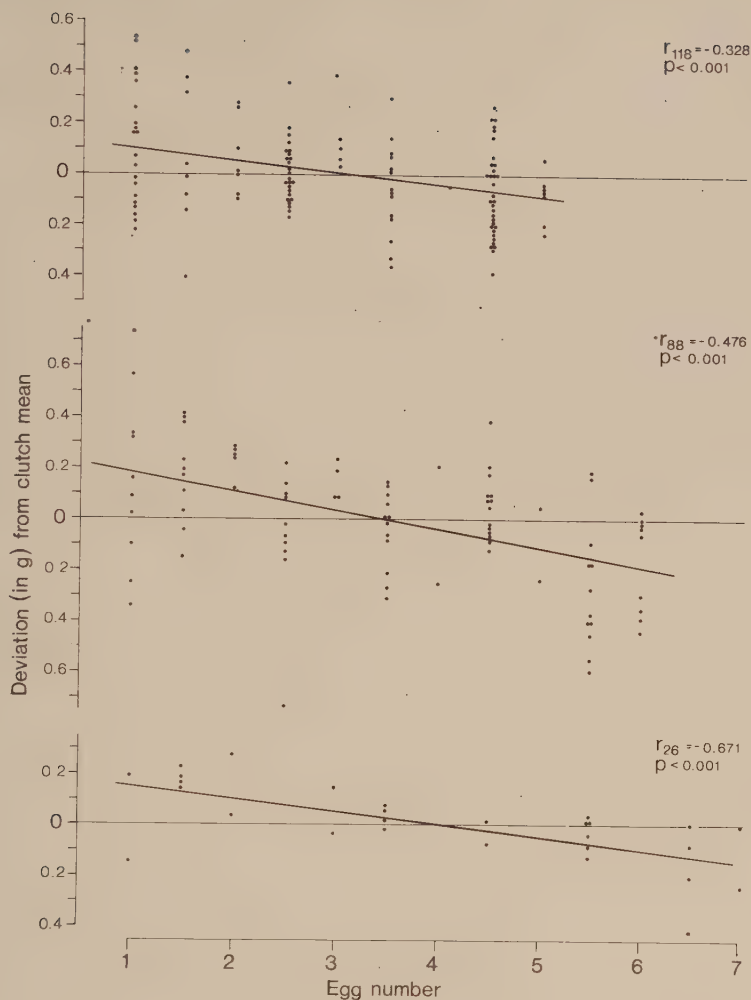


Fig. 1. Variation in egg weight with laying sequence in the Starling. The deviation of each egg from the mean egg weight in the clutch is plotted against its sequence number in the laying. Data from V. Tvet (n=15) and Sjötorp (n=39) in 1982.

Äggviktens variation med äggets nummer i läggningssekvensen. Varje äggs avvikelse från medelvikten i kullen är avsatt mot nummer i sekvensen. Uppgifter från V. Tvet (n=15) och Sjötorp (n=39) 1982.

	First egg	Last egg
Heaviest	17	0
Intermediate	12	13
Lightest	7	9
Total	36	22

Tab. 2. Weight relations of the first and the last egg in the laying sequence.

Första och sista äggets relativa vikt inom kullen.

Tab. 3. Mean intra-clutch and inter-clutch variation (C.V. in %) in egg weight in clutches of different size. The number of clutches is given in parenthesis.

Variation i äggvikt inom och mellan kullar av olika storlek (mätt som variationskoefficienten, %). Antalet kullar anges inom parentes.

		Clutch size		1981	1982			
					Sjötorp		V. Tvet	
Intra-clutch variation	4	3.30	(7)	-	(-)	-	(-)	
(Inomkulls-variation)	5	3.34	(26)	2.94	(19)	2.41	(5)	
	6	3.69	(29)	3.60	(10)	3.57	(6)	
	7	3.20	(4)	1.93	(3)	3.18	(1)	
Inter-clutch variation	4	5.56	(7)	-	(-)	-	(-)	
(Mellankulls-variation)	5	5.69	(26)	6.57	(19)	8.61	(5)	
	6	7.99	(29)	7.88	(10)	6.18	(6)	
	7	6.26	(4)	3.70	(3)	-	(-)	

pair of eggs plotted in intermediate positions). Although the spread is considerable, the trend is clear; egg weights decreased with laying order. Since they tended to be constant in relation to date of laying or, if anything, to increase, the observed decrease with laying order is likely to be real. Furthermore, eggs lose weight during incubation (by about $2\% d^{-1}$ according to data in Murton & Westwood 1977). Since incubation in the Starling seems to commence after the fourth egg is laid (Kessel 1957, Dunn et al. 1979), the differences in weight between the first and the last eggs should be still larger than those we recorded. The first egg in the sequence was not invariably the heaviest, however, nor was the last one always the lightest (Tab. 2).

Variation in egg weight between and within clutches

As shown above, mean egg weight varies both between and within clutches. This variation is summarized in Tab. 3. The inter-clutch variation is, on average, larger than the intra-clutch variation, the C.V. values varying between 3.7 and 8.6 % for the former and between 1.9 and 3.7 % for the latter.

DISCUSSION

In the following discussion we use the term weight indiscriminately also for instances when volumes were actually given in the original references, because correlations between these two measures are normally linear and very high (Sternberg & Winkel 1970, Pikula 1971, van Noordwijk et al. 1981). Egg weight is, potentially or actually, influenced by a number of factors, which may be more or less interdependent, such as ambient temperature, clutch size, laying date, and laying sequence. Nevertheless we will consider some of them separately.

Egg weight in relation to laying date

Egg weights vary with laying date differently in different species. In *Parus major*, *Fringilla coelebs*, *Turdus philomelos* and *Agelaius phoeniceus* they increase in the course of the breeding season (Perrins 1970, Svensson 1978, Pikula 1971, Holcomb 1969), whereas they decrease in *Columba palumbus* and *Troglodytes aedon* and, weakly, in *Calcarius lapponicus*, *Plectrophenax nivalis*, and *Spinus tristis* (Murton et al. 1974, Kendeigh 1941, Hussell 1972, Holcomb 1969). Rydén (1978) recorded a broad range of egg weights in *Turdus merula* with some tendency towards a peak midway in the nesting season, while Sternberg & Winkel (1970) in *Ficedula hypoleuca* and Bryant (1978) in *Delichon urbica* failed to find any trend. In those cases when egg weights have increased in the course of the season, a simultaneous decrease in clutch size has been observed.

There is reason to believe that the pattern in which egg weights change through time in different species evolved as a response to the environmental conditions each species faces. The amount of provisioning of the eggs (egg weight) affects the size and the survival probabilities of the hatchlings (Parsons 1970, 1975, Nisbet 1973, Pinkowski 1975, Howe 1976, O'Conner 1979, Lundberg & Väisänen 1979, Ankney 1980) and the survival probabilities

are rarely if ever constant through the entire breeding season. The best demonstration of the changing advantage of laying large eggs is the study of *Parus major* by Schifferli (1973). As noted above, in this species egg weight increases during the breeding season. Schifferli showed that egg weight strongly influenced survival in late broods, whereas it had no effect on broods started early in the season. Also Murton et al. (1974) discuss the possibility that egg weight in the Woodpigeon is adjusted to the feeding situation at the time the young are in the nest. A large egg early in the season could be seen as an insurance against the poorer feeding conditions prevailing at that time. But the authors also discuss other, non-adaptive, explanations for the observed changes in egg weight.

Egg weight in relation to clutch size

The data of Tab. 1 indicate a weak decrease of mean egg weight with increasing clutch size in our Starlings, but they are unsuitable for a more detailed analysis. It should be pointed out, however, that our results contrast with those of Ojanen et al. (1978); their Fig. 4 indicates that eggs were largest in clutches of 7.

The relationship between egg weight and clutch size apparently varies considerably between species; a positive correlation was found in *Troglodytes aedon* (Kendeigh et al. 1956) and, although weak, in *Calcarius lapponicus* and *Plectrophenax nivalis* (Hussell 1972); a peak in egg weight in clutches of intermediate size was found in *Parus major* and *P. caeruleus* (Gibb 1950, Busse 1967, Winkel 1970; but cf. Ojanen et al. 1978); in *Turdus philomelos* (Pikula 1971), *Delichon urbica* (Bryant 1978) and *Ficedula hypoleuca* (Sternberg & Winkel 1970) no correlation was found; in the latter species, however, Ojanen et al. (1978) demonstrated a decrease with clutch size, and negative correlations were also found in *Melospiza melodia* (Nice 1937) and *Agelaius phoeniceus* (Holcomb 1969).

It is very difficult to evaluate the contrasting results obtained for different species (and sometimes for the same species in different studies).

Egg weight in relation to ambient temperature

The fact that we did not find any correlation between egg weights and mean ambient temperatures on the 1 to 7 days preceding the laying of the eggs does not, of course, exclude the possibility

that egg weights are influenced by ambient temperatures; indeed such an influence has been documented (Jones 1973, Howe 1978, O'Connor 1979, Ojanen et al. 1981). Thus, Howe (op.cit.) found a weak effect of temperature during the day yolk was supposed to be formed and Ojanen et al. (op. cit.) similarly found a positive influence on egg weight of ambient temperature 1-3 days prior to the laying of the egg in *Parus major* and *Ficedula hypoleuca* but this applied only to the last egg in the laying sequence. They thought this egg to be more sensitive to external influences because the female would have exhausted her reserves in the course of laying the clutch. In *Sturnus vulgaris* they found a strong positive correlation with temperatures 7 days before laying.

It is well established that gaps in the laying sequence sometimes occur after unusually adverse weather, including low temperatures (see e.g., Winkel 1970 for references), and Jones (1973) suggested that there is a lower threshold value for the size of an egg below which hatchability and survival are drastically reduced. When resources are inadequate for the formation of an egg of this minimum size the female suspends laying. Clearly, however, much more detailed information is needed on the influence of small variations in ambient temperature on both food availability and the energetics of egg formation.

Egg weight in relation to laying sequence

In a few non-passerines and in most passerines where the relationship between egg weight and laying order has been studied, egg weights have tended to increase in the laying sequence (see Ojanen et al. 1981, Tab. 9; to their list of species exhibiting increasing egg weights can be added another study of *Ficedula hypoleuca* (Hanson et al. 1966) and a laboratory study of *Lonchura striata* (Jefferies 1969)). While the last egg is the smallest at least in some ducks (Koskimies 1957) and geese (Manning 1978) and in a number of gulls and terns (Paludan 1951, Gemperle & Preston 1955, Ytreberg 1956, Behle & Goates 1957, Coulson 1963, Harris 1964, Barth 1967, Vermeer 1969, Parsons 1970, 1972, 1976, Nisbet 1973, Ryder 1975, Nisbet & Cohen 1975, Gochfeld 1977, Ricklefs et al. 1978, Lundberg & Väisänen 1979), it seems to be rare in passerines that egg weights decrease with laying order. The only possible examples we have found are the Redstart *Phoenicurus phoenicurus* (Ojanen et al. 1981) and the Red-winged Blackbird (Holcomb & Twiest in Holcomb 1969). The results for the Starling in this

study therefore may seem surprising (Fig. 1).

Two main categories of explanations of this observation can be distinguished: either the decrease is non-adaptive, i.e. reflects external or internal influences that have either neutral or negative effects on the production of young, or it is adaptive, i.e. evolved because it normally gives rise to the largest number of surviving offspring.

In the first case, one hypothesis is that the laying female draws, at least partly, upon body reserves either in the form of energy or specific nutrients when forming eggs, and that these reserves are gradually being depleted in the course of laying. It is, however, not at all obvious why she should be unable to distribute these reserves equally on the eggs of her clutch. As a matter of fact, Schifferli (1980) showed that female House Sparrows *Passer domesticus* accumulate fat shortly before they start laying eggs and that they draw heavily on these reserves during laying. Still the House Sparrow's last egg is the heaviest in the clutch (Murphy 1978; but this may not be universal: Dawson (1972, cited in O'Conner 1979) reported that the final egg of the clutch was the lightest). Furthermore, the smaller size of the third egg in the Herring Gull *Larus argentatus* is not the result of depletion of reserves since the removal of eggs induced gulls to lay much larger clutches than normal without the decrease in size characteristic of the third egg (Paludan 1951, Parsons 1976). Hence it is perhaps more likely that the decrease in egg weight with laying order that we observed in the Starling represents an adaptation.

Hatching normally takes place in the order that the eggs were laid, at least for those laid after regular incubation started. The increase in egg weight with laying order observed in most passerines so far studied (i.e. the reverse from the situation in our Starlings) has been interpreted as an adaptive mechanism that mitigates the effects of asynchronous hatching. This interpretation of adaptive egg size variation should apply whether hatching asynchrony evolved to minimize losses due to predation (Clark & Wilson 1981), to reduce peak food demands of the brood (Hussell 1972, Bryant & Gardiner 1979, Parsons 1975), or, as most commonly assumed, to enable the selective starving of young in case of food shortage (Lack 1954, O'Conner 1977, and others). In the last case, a large egg resulting in a heavy chick (Jones 1973, Schiff-erli 1973, Pinkowski 1975, Ricklefs et al. 1978, O'Conner 1979)

would enable the last-hatched young to stay alive for as long as possible, while still leaving the parents with the option for selectively reducing their brood should feeding conditions deteriorate (Howe 1976, 1978, Rydén 1978, Bengtsson & Rydén 1981). Thus, these authors view the increase in egg weights with laying order as a supplementary adaptation to asynchronous hatching and in a way working in the opposite direction; this idea has been criticized by Clark & Wilson (1981). Anyway, hatching in the Starling is relatively asynchronous. Regular incubation starts after the fourth egg (Kessel 1957, Dunn et al. 1979; but cf. Tinbergen 1981), and in our study there were considerable age (and size) differences within the broods. Brood reduction also took place, being of similar magnitude in broods of different size. Lumping material from several years, hatchability was close to 90 % for clutches of 4 to 7. The proportion of young dying between hatching and fledging were 33, 16, 12, and 12 % for initial clutches of 4, 5, 6, and 7 eggs, respectively. Therefore, if eggs hatch in the order they are laid, the decrease in weight with laying order should make initial differences between nestlings in a brood more, not less, pronounced.

There is, however, the alternative possibility that the smaller size of the late-laid eggs decreases their incubation time (Bryant 1975) resulting in a more synchronous hatching of the clutch than would otherwise have been the case. If so, the laying of progressively smaller eggs could be seen as a means of reducing the period that the nest is in use without reducing clutch size.

In summer then, provided the observed trend in egg weights is adaptive, we are left with two contrasting hypotheses. Either selection has favoured the creation of large differences in competitive ability between siblings by the combined effects of egg size variation and hatching asynchrony, or egg weight differences are a means of reducing nesting time without reducing clutch size. Clearly, both better data and experimentation are called for. Finally, the great variability (Fig. 1, Tab. 2) needs explanation.

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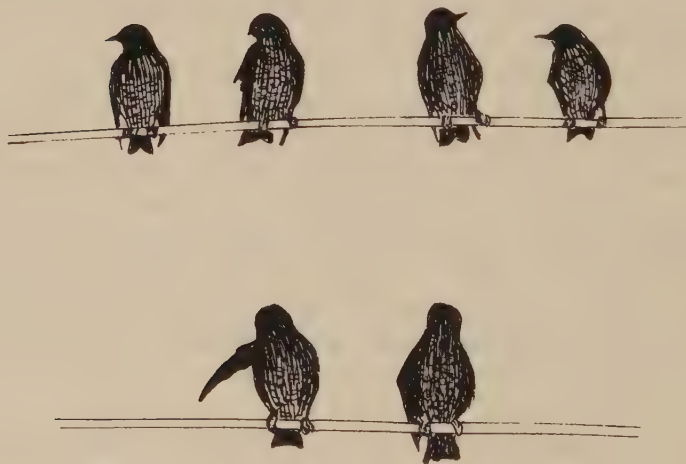
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SAMMANFATTNING

Vikten hos starägg undersöktes under ett par års tid. Resultaten kan sammanfattas i följande punkter: (1.) Det finns ingen klar tendens till någon förändring av äggvikten med datum för läggningen. (2.) Det finns inget samband mellan äggens vikt och temperaturen under de sju dagarna närmast före läggningen. (3.) Det föreligger ingen signifikant minskning av äggvikten med ökande kullstorlek. Dock finns det en "tendens" till att vikten på äggen i den största kullen alltid är mindre än hos övriga kullar. (4.) Det finns en klar tendens till att äggvikten minskar med läggningsordningen inom kullen. Denna tendens är av samma omfattning i kullar av olika storlek.



Clutch size in relation to nest-box area in the Starling *Sturnus vulgaris*

Kullstorlek hos staren i relation till holakens yta

INTRODUCTION

In some non-determinate layers, clutch size may vary with a factor of about two. Many of the reasons for this variation have been carefully investigated for many decades. Factors such as the quality of the individual bird and of the environment have been shown to influence the clutch size (for a review, see Klomp (1970)).

THE 'AREA-EFFECT' ON CLUTCH SIZE

Data have accumulated during the last few years which show that, in hole-nesting birds, certain qualities of the nest cavity may influence clutch size. Thus, since 1973, significant correlations between the bottom area of the nest cavity and the clutch size have been obtained in some small passerines. Furthermore, at the International Ornithological Congress in Berlin in 1978, information was presented which showed that the insulation of the nest-box can also influence the clutch size; the better insulation the less energy expenditures of the female roosting or resting in the box, resulting in an energy gain for these females compared with females in less well insulated boxes, which allows the former to lay larger clutches.

Karlsson & Nilsson (1977) reviewed the data available on the relation between clutch size and bottom area of the nest cavity and provided linear regressions for each year and species (see Tab. 1 in that paper). Here I used these values to calculate a mean value of the slopes for each species (Tab. 1).

The figures in Tab. 1 give rather clear-cut evidence for the existence of an area-effect on clutch size in the marsh tit *Parus palustris*, the willow tit *P. montanus*, and the great tit *P. major*. The pied flycatcher *Ficedula hypoleuca* does not respond so strongly, but all regressions are positive and two are also statistically significant.

Tab. 1. Generalized data on the relation between clutch size and bottom area of the nest-cavity in some hole-nesting passerine species (data from Karlsson & Nilsson (1977) and this study).
Generaliserade uppgifter om sambandet mellan kullstorlek och bottenyta i bohålorna för några tättingar (uppgifter från Karlsson & Nilsson (1977) samt denna uppsats).

	No of studies Antal studier	Mean of the slopes (eggs/cm ²) Medeltal för lutningar (ägg/cm ²)	Bottom areas cm ² Bottenytor cm ²	
Marsh tit <u>Parus palustris</u>	1	0.117	natural holes <i>naturliga bohål</i> , approx. 25-65 cm ²	Highly significant relation <i>Höggradigt signifikant</i> (Ludischer 1973)
Willow tit <u>Parus montanus</u>	1	0.072	ditto	ditto
Great tit <u>Parus major</u>	4	0.023	57, 72, 87, 103, 104, 110, 125	Highly signif. in all cases <i>Höggradigt sign. i alla fall</i> (Johansson 1974, Nilsson 1975, Karlsson & Nilsson 1977. See also Graczyk 1967 and Löhrl 1973)
Pied flycatcher <u>Ficedula hypoleuca</u>	5	0.009	57, 72, 87, 103, 104, 110	Positive corr. in all cases but only statistically sign. in two <i>Positiv korr. i alla fallen, men endast statistiskt sign. i två</i> (Johansson 1974, Nilsson 1975, Karlsson & Nilsson 1977)
Starling <u>Sturnus vulgaris</u>	3	0.001	120, 144, 225	No Relation <i>Inget samband</i> (Data from this paper)

Tab. 2. Breeding data for starlings *Sturnus vulgaris* in a colony provided with nest-boxes of three different sizes. Day 0 = 29 April.
 Häckningsdata för starar i en koloni som erbjuddes tre olikstora holkar. Dag 0 = 29 april.

	large boxes (15x15 cm)				medium boxes (12x12 cm)				small boxes (10x12 cm)			
	n	mean clutch size	SE	date for the first egg	n	mean clutch size	.SE	date for the first egg	n	mean clutch size	SE	date for the first egg
1974	13	5.08	1.12	0.7	10	5.30	0.48	0.4	9	5.00	1.00	0.9
1975	11	5.45	0.82	3.8	10	5.50	0.53	2.8	12	5.33	0.49	3.1
1977	10	5.60	0.84	5.4	13	5.54	0.66	4.8	13	5.15	0.90	5.7

The figures in Tab. 1 give rather clear-cut evidence for the existence of an area-effect on clutch size in the marsh tit Parus palustris, the willow tit P. montanus, and the great tit P. major. The pied flycatcher Ficedula hypoleuca does not respond so strongly, but all regressions are positive and two are also statistically significant.

CLUTCH SIZE AGAINST NEXT-BOX AREA IN THE STARLING

Square-shaped, wooden nest-boxes with a bottom area of 10 x 12, 12 x 12, and 15 x 15 cm, respectively, were put up in the trees and on the buildings of an abandoned farm in an open grass-land in Skåne, South Sweden (55° 44' N, 13° 28' E). Boxes of different size alternated; in all 45 boxes were erected on an area 50 x 50 m. Data on the onset of laying and on clutch size were collected by daily inspections of the boxes. Mean clutch size and mean date for the laying of the first egg in the three types of boxes during three years are given in Tab. 2.

As can be seen from the table, there is no consistent relationship between nest-box area and clutch size in the starling. A linear regression analysis of clutch size (y) against nest-box area (x) gives the following slopes of the lines:- 0.0003, 0.0007, and 0.0034 (resulting in the mean value of 0.001 presented in Tab. 1). These relations are far from statistically significant!

The evaluation of the data is somewhat complicated because, among other things, clutch size decreases with about 0.3 eggs/day. A compensation for this decrease does not, however, change the conclusion that no correlation between clutch size and bottom area of the nest cavity exists in the starling, at least not within the box sizes used in the present study.

DISCUSSION

No solid explanation why the clutch size of some passerine species increases with increasing area of the nest cavity has been put forward, nor one that explains why some species react very strongly as, e.g. the marsh tit, in which clutch size doubles with a doubling in the area of the nest cavity, whereas the clutch size of other species like the starling is not influenced at all. The

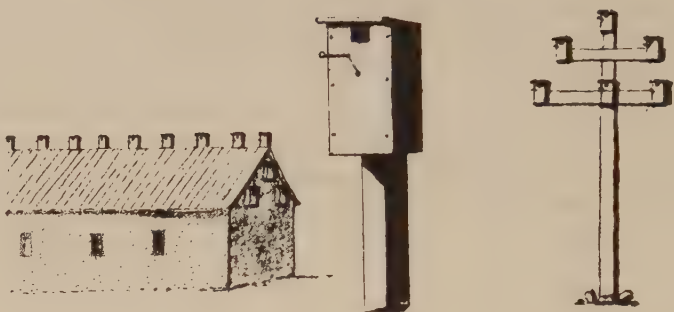
following suggestions have been offered: (1) a larger clutch can be produced in larger boxes due to better insulation of the eggs (by a thicker layer of nest-material) (Löhr 1973), (2) in a larger box the nestlings can spread out on hot days and avoid hyperthermia, (3) the amount of energy lost from a brood will be affected by the proportion of the nest cavity that the brood occupies, suggesting that the weight of a species in combination with the size of the nest cavity may be important factors which determine how sensitive the species is to changes in bottom area. A further discussion of these suggestions is found in Karlsson & Nilsson 1977.

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SAMMANFATTNING

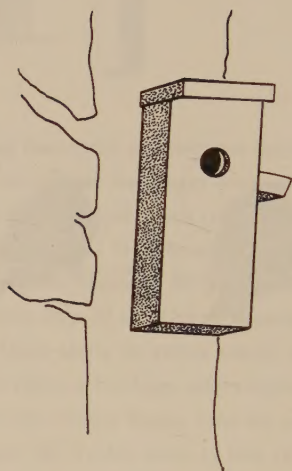
Vissa hålhäckare såsom entita, tallita, talgoxe och svartvit flugsnappare lägger större kullar ju större bokammarens bottenyta är (Tab. 1). En treårig undersökning av staren visar att denna skiljer sig från ovannämnda arter genom att kullstorleken inte varierar med holkarnas bottenyta (Tab. 2).

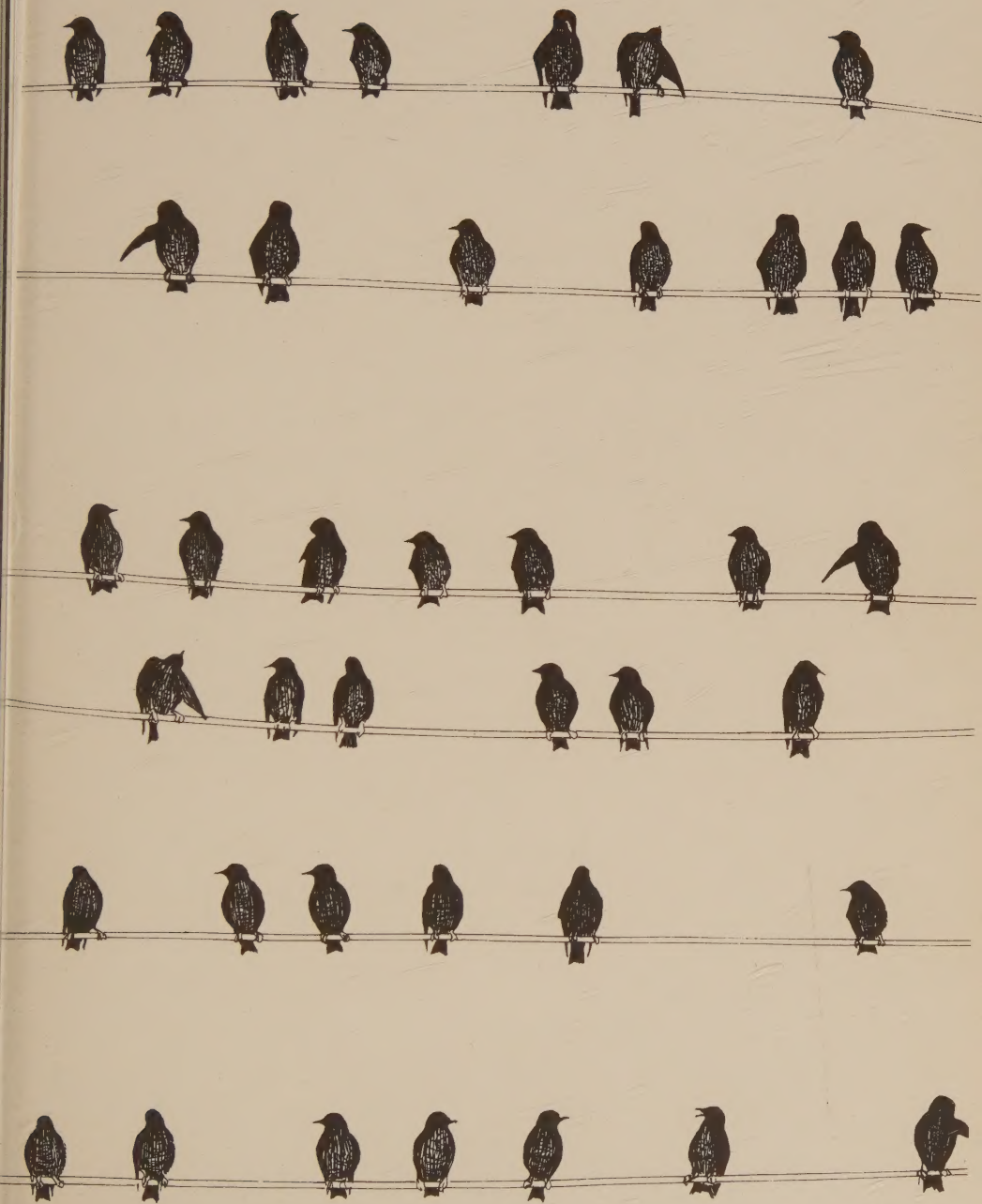


"Både i Visby och öfverallt hvar jag framfarit, på Gottland hafva folket Machiner utsatta, till att låta Starar bygga bo uti - då man tager ungarne till mats såframt de blifva flygfärdige. Desse kallas Stare Stuncker och finnas Sådane uppsatte på husgaflarne, ofta hela ryggåsen utåt, äfven i Trädgårdar, i Trån, Samt på Häkar utmed gärdesgårdar, ibland helt nära under fönstren, för att höra sången af dessa foglar. - Vid en gård kan ibland finnas 20 a 30 stn Sådane utsatte Stuncker, ja ända till 100etals på stora gårdar. Man tager aldrig de gamle starar, endast de unge och af första kullen - då de gamle åter värpa och utligga andra kullen, endast att alla de första borttagas, att ingen kommer ut eller undan. Man har sedan sagt mig, att man af 1-st kullen bör lämna ett par för afvelns skull, ty lika väl värpa de igen merendels andra kulln. Machinen göres af 4 hopspikade NB gamla brädlappar, litet öfver 1/2 aln långa och 7 a 8 tum breda med botten ofvan och nedan, Som ett litet Skåp. Den öfre botten eller Taket, som bör vara rörligt och endast medelst en Spik eller pinne baktill fäst, bör stå litet öfver på framsidan till Skjul för ett litet hål. --- Man iakttagert att sätta en näsduk i hålet, då man vill skatta boet. Man brukar äfven en skjutlucka för hålet, som med ett streck bakifrån kan tilldragas om man vill taga de gamle stararne med. Staren har 6 a 7 ungar."

G. Hilfelings journal öfver En Resa genom Småland, Öland och Gottland under Sommaren år 1797. Manuskript, Kungl. Biblioteket.







A handwritten musical score on eight staves. The notation is in treble clef with a common time signature (C). The music features various note values including eighth and sixteenth notes, as well as rests. The first staff begins with a key signature change from one sharp (F#) to two sharps (F# and C#). The third staff includes first and second endings, marked with '1' and '2' and a repeat sign. The fifth staff concludes with the word 'Fine'. The eighth staff concludes with the instruction 'D.S. al Fine'. The handwriting is in dark ink on aged, slightly yellowed paper.

Fine

D.S. al Fine